University of Alberta

Growth-climate relationships of lodgepole pine in Alberta

by

Sophan Chhin

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Abstract

A dendrochronological approach was used in this dissertation to identify the principal climatic factors that have influenced the interannual, historical pattern of lodgepole pine (*Pinus contorta* var. *latifolia*) growth in Alberta. A network of 17 lodgepole pine sites in Alberta was examined in the cordilleran forests along the eastern slopes of the Rocky Mountains and in western Cypress Hills. The results suggested that heat and moisture stress in late summer of the previous growing season, cold and snowy winters, and the length of the current growing season are important determinants of the radial growth of lodgepole pine in Alberta.

An expanded network of 65 lodgepole pine sites was examined to identify the relationships between climate and basal area growth of lodgepole pine across four elevational ecoregions (Boreal Highlands, Foothills, Rocky Mountains, Cypress Hills) and four diameter size classes. Growth was inhibited by low temperature in all winter months at the most northern Boreal Highland sites which had the coldest winters, but this effect was interrupted in some of the midwinter months in the more southerly sites in the Rocky Mountains, and it is postulated this was due to the damaging influences of Chinook winds. The results indicated that it is sufficient to sample only the largest diameter trees in a stand to provide insight into growth-climate relationships. Forecasted growth estimates indicated that future climate warming will negatively impact the productivity of lodgepole pine in the foothills.

Based on detailed stem analysis, this dissertation also tested the hypothesis that ring growth at the upper part of the bole of trees is affected by climatic conditions

differently than rings formed at breast height. Growth at lower sections of the bole was driven mainly by temperature and moisture conditions in the seasons leading up to the start of the growing season in the year of ring formation, while the upper part of the bole was more related to conditions in the year of growth. The magnitude of the expected decline in the foothills under scenarios of future climate change was more pronounced based on the growth-climate models for the whole stem versus estimates from breast height only.

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Chapter I: General Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) represents a significant component of Alberta's forest resources, and is a key contributor to Alberta's forest industry, accounting for approximately 40% of the annual harvest in the province (Huang et al. 2001). Lodgepole pine forests also contribute to the maintenance of other forest values such as providing protective cover for the vital watersheds along the eastern slopes of the Rocky Mountains. There is growing concern of the potential vulnerability of Alberta's forests to future climate change, in particular the projected increases in temperature (Alberta Environment 2007). To ensure the sustainable management of lodgepole pine forests, it is important to quantify what potential impact a warmer climate and changes in moisture conditions can have on future productivity.

Vegetation – Climate Relationships

It is generally accepted that plants respond to climate and climate is considered a dominant factor governing the geographical distribution of plants (Woodward 1987). Early biogeographers constructed vegetation classification systems primarily on the basis of climate variables; e.g., mean annual temperature, mean annual precipitation and mean annual potential evapotranspiration are utilized in Holdridge's (1947) system of world vegetation classification (MacDonald 2003). Similarly, the ecological classification scheme in Alberta is based partly on climatic variables which include mean annual temperature, mean annual precipitation and growing degree-days greater than 5°C (Natural Regions Committee 2006). The biogeographical distribution of conifer species

in Canada corresponds well with spatial patterns in climatic factors. For instance, the northern limit of some conifer species generally coincides with the 10°C July-isotherm (MacDonald 2003), while the zero isoline of precipitation minus potential evapotranspiration corresponds generally with the southern boundary of major boreal conifer species in western Canada (Hogg 1994).

Climate affects physiological and biochemical processes involved in plant growth (Kozlowski et al. 1991; Larcher 2003). Many metabolic processes in plants, but in particular photosynthesis and respiration, are temperature dependent. The temperature response pattern of photosynthesis is generally parabolic in which photosynthetic rates peak at an optimum temperature, but as rates of maintenance respiration generally increase with increasing temperature, net photosynthesis declines. Water is the main chemical component of most plant cells, is the medium for biochemical reactions, and is required for the maintenance of cell turgor and cell enlargement. Water stress, by limiting cell enlargement and growth, generally reduces leaf area and thus limits photosynthetic production. More importantly, water stress also leads to stomatal closure which in turn limits CO_2 uptake and thus reduces photosynthesis and growth. Temperature also influences the water balance of plants since high temperatures are often associated with high vapour pressure deficits that can lead to increases in potential water loss from evapotranspiration.

Impacts of Climate Change on Forests

The instrumental climatic record has indicated that global average surface temperatures have increased by 0.74°C over 1906-2005 (IPCC 2007). Eleven of the 12

years between 1995 and 2006 are ranked within the 12 warmest years since 1850, with 1998 and 2005 being the warmest two years. Proxy climate data for the Northern Hemisphere has indicated that the rate of warming in the second half of the 20th century has been the greatest for any 50-year period in the past 1300 years (IPCC 2007). The 20th century warming trend has been induced by increases in greenhouse gases, most notably CO_2 released primarily as a result of anthropogenic activities (fossil fuel use and land use changes such as tropical deforestation). Although precipitation has increased regionally over the 20th century including the eastern parts of North America; the intensity, duration and spatial coverage of droughts has also increased, leading to wide-spread tree mortality in some forest types (Breshears et al. 2005). Moderate climatic warming over areas that are low-temperature limited and not affected by water limitations, have generally showed increased forest productivity since the middle of the 20th century (Boisvenue and Running 2006).

Regionally, the impacts of recent climate change have been most apparent in northern regions (IPCC 2007) and in mountainous areas including the cordilleran forest of western Canada (Luckman 1998). The forests of the cordilleran region provide opportunities to document past relationships between tree growth and climate which in turn will help provide insight into how the productivity of these forests might be affected by future climatic change. Seasonally, the effects of recent climate change have been most apparent during the winter and spring. These regional and seasonal changes in climate are expected under projections of future climate change.

Projections of future climate change based on general circulation models and different emission scenarios of greenhouse gases indicate a further warming of 1.1°C–

6.4°C by the end of the 21st century (2090-2099) relative to 1980-1999 (IPCC 2007). Climate models also forecast increased summer dryness in some regions since temperature-induced increases in potential evapotranspiration could outweigh expected future increases in precipitation. Large-scale vegetation-climate models forecast poleward and altitudinal shifts in biomes (Fischlin et al. 2007); however, there is limited understanding of the key climatic factors that affects the biology of the constituent plant species. It is expected that trees species will respond differentially to climate change (Kirschbaum and Fischlin 1995). Consequently, it is important to understand the climatic response pattern of tree species in order to begin assessing the potential impacts of climate change on forest distribution and productivity.

Dendrochronological Approach

There are a number of different approaches to examine the response of tree populations to climate (Brubaker 1986). The paleoecological approach has focused on examining fossil pollen records in lake sediments, and palynology has provided insight into millennial-scale forest dynamics that have related tree-range expansions with climate change (Woodward 1987). Other methodological approaches rely on the tools of dendrochronology which involves the crossdating and measurement of annual growth rings in mainly temperate and boreal trees which in turn allows the determination of tree ages and past growth rates (Fritts 1976). Tree ages provide the basis for demographic studies by which tree age structures are related with climatic records. Similarly, dendroclimatic studies typically involve comparing the sequence of relative ring-width patterns with instrumental climate records.

Crossdating is the most important principle guiding the practice of dendrochronology (Fritts 1976). In general, crossdating is the procedure of synchronous matching of ring-width variations among trees that have grown in nearby areas in order to identify the exact year in which each ring was formed (Fritts 1976). Synchronous growth patterns among trees is considered a reflection of a limiting external environmental factor (e.g., climate). Lack of synchrony between trees can point to incorrectly dated tree-rings and the presence of ring anomalies such as missing rings or false rings.

The traditional approach of dendroclimatology has been focused on the use of tree rings for reconstructing past climatic conditions (Fritts 1976). For this purpose, trees near the limits of their ecological tolerance and geographical distributions are preferred because they are generally considered to be more sensitive to climatic factors (Schweingruber et al. 1990). The limitations of this traditional dendroclimatic approach, however, is that growth-climate relationships at environmental extremes, in marginal sites may not be representative of growth responses to climate near the center of a tree species distributions where forest productivity is usually greater. Trees establishing in open grown conditions are preferred over those in closed-canopy conditions in order to minimize the influence of competition related to changes in stand density (Schweingruber et al. 1990). Further, trees are traditionally sampled at breast height from the largest diameter size classes. However, growth responses to climate at breast height of the largest diameter trees might not be representative of other portions of the tree stem and smaller diameter size classes.

Lodgepole Pine Autecology

Lodgepole pine has a broad distribution in western North America due to its wide ecological amplitude and its ability to grow over a wide range of climatic conditions (Lotan and Critchfield 1990). It is highly shade intolerant, usually succeeded by more shade tolerant competitors and thus it is considered to be a fire-maintained subclimax species. Its serotinous cones release a copious amount of seed after fire to form high density stands of lodgepole pine. Subsequent stand development in lodgepole pine, as in most even-aged stands following a major stand-replacing disturbance, typically involves natural self thinning and diameter size differentiation due to intraspecific competition mainly for light (Oliver and Larson 1996). In the western Canadian province of Alberta, lodgepole pine is the predominant forest type in the cordilleran forests along the eastern slopes of the Rocky Mountains (Huang et al. 2001). Lodgepole pine is naturally absent from most of eastern Alberta, with the exception of a few disjunct populations including one in the western Cypress Hills (Henderson et al. 2002).

Most previous studies examining the influences of climate on the radial growth of lodgepole pine have been conducted at specific locations (1-4 sites) and (or) of limited regional extent in the United States (Villalba et al. 1994; Sauchyn and Skinner 2001; Sauchyn et al. 2003; Case and Peterson 2007) and Canada (Sauchyn et al. 2002; Sauchyn et al. 2003). Consequently, understanding of radial growth responses to climate in lodgepole pine is lacking at larger regional scales.

Height growth studies of lodgepole pine in the cordilleran forest region of Alberta indicate that site index (i.e., height growth over the first 50 years of growth) of lodgepole pine is positively associated with warm, early springs and warm growing seasons

(Monserud et al. 2006). Height growth of lodgepole pine in British Columbia generally increased with increasing mean annual temperature; in addition, height growth was also negatively affected by measures of annual moisture deficiency (Nigh et al. 2004; Wang et al. 2006). Height growth is considered the best indicator of site potential and is not generally sensitive to stand conditions. However, height growth patterns are not usually resolved to an interannual temporal resolution, but are instead usually collapsed to the single value of site index. Consequently, site index – climate relationships can not be examined at the interannual temporal scale. That is, in height growth studies with many site index observations from numerous sites, spatial trends in growth-climate relationships serves as a proxy for temporal trends (Nigh et al. 2004; Wang et al. 2006). Although diameter growth is sensitive to stand conditions (e.g., stand density), the advantage of diameter growth is that it can be resolved to a fine scale of temporal resolution (interannual scale). Examining interannual variations in volume increment via stem analysis is useful to examine whole stem growth patterns and thus integrate both radial and height growth responses. However, there have been few attempts to relate interannual variations in volume increment with climate data for tree species in general, and such analyses are absent entirely for lodgepole pine. The paucity of detailed stem analysis studies to determine interannual volume increment is partly due to the fact that such studies require destructive sampling, and that subsequent sample processing (i.e., sanding) and detailed annual tree ring measurement is extremely resource intensive (LeBlanc 1990).

Research Objectives

The general objective of this dissertation is to identify the principal climatic factors (i.e., temperature and precipitation) that have influenced the historical pattern (over the 20th century) of growth of lodgepole pine in the cordilleran forests of Alberta. Chapter II explores the climatic response of ring-width in lodgepole pine from a network of 17 sites based on increment cores sampled at the traditional breast height. Chapter III documents the climatic response of basal area increment at breast height of lodgepole pine across diameter size classes and ecological regions, and over a broader area consisting of a network of 65 sites. Chapter IV examines differential responses to climate primarily between the upper and lower stem of lodgepole pine. In addition to basal area increment, the measures of growth considered in Chapter IV also include interannual volume increment. Projections of growth under future climate change scenarios in the 21st century are also examined in both Chapters III and IV.

References

Alberta Environment. 2007. Facts about climate change [online]. Alberta Environment, Edmonton, Alberta. Available from http://www3.gov.ab.ca/env/climate /docs/Fact_Book.pdf [accessed 2007 May 15].

Boisvenue, C., and Running, S.W. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Global Change Biology, **12**: 862-882.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences U.S.A., **102**: 15144-15148.

Brubaker, L.B. 1986. Responses of tree populations to climatic change. Vegetatio, **67**: 119-130.

Case, M.J., and Peterson, D.L. 2007. Growth-climate relations of lodgepole pine in the North Cascades National Park, Washington. Northwest Science, **81**: 62-75.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J., and Velichko, A.A. 2007. Ecosystems, their properties, goods, and services. *In* Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel of Climate Change. *Edited by* M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson. Cambridge University Press, Cambridge, UK. pp. 211-272.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, UK.

Henderson, N., Hogg, E.H., Barrow, E., Dolter, B. 2002. Climate change impacts on the island forests of the Great Plains and the implications for nature conservation policy: the outlook for Sweet Grass Hills (Montana), Cypress Hills (Alberta-Saskatchewan), Moose Mountain (Saskatchewan), Spruce Woods (Manitoba) and Turtle Mountain (Manitoba-North Dakota). Prairie Adaptation and Research Collaborative (PARC), Regina, Saskatchewan, Final Rev. Report.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Canadian Journal of Forest Research, **24**: 1835-1845

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. Science, **105**: 367-368.

Huang, S., Morgan, D.J., Klappstein, G., Heidt, J., Yang, Y., and Greidanus, G. 2001. Yield tables for seed-origin natural and regenerated lodgepole pine stands. Alberta Sustainable Resource Development, Edmonton, Alberta. Tech. Rep. Pub. No. T/485.

IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge University Press, Cambridge, UK.

Kirschbaum, M.U.F., and Fischlin, A. 1995. Climate change impacts on forests. *In* Climate change 1995: impacts, adaptation and mitigation of climate change. Contribution of Working Group II to the Third Assessment Report of the

Intergovernmental Panel on Climate Change. *Edited by* R.T. Watson, M.C. Zinyowera, and R.H. Moss. Cambridge University Press, Cambridge, UK. pp. 95-129.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 4th Ed. Springer, Berlin.

LeBlanc, D.C. 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Canadian Journal of Forest Research, **20**: 1399-1407

Lotan, J.E., and Critchfield, W.B. 1990. *Pinus contorta* Dougl. Ex. Loud. or Lodgepole pine. *In* Silvics of North America: 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv., Washington, DC. Agric. Handbook 654. pp. 302-315

Luckman, B.H. 1998. Landscape and climate change in the central Canadian Rockies during the 20th century. Canadian Geographer, **42**: 319-336.

MacDonald, G.M. 2003. Biogeography: space, time and life. John Wiley and Sons, New York, NY.

Monserud, R.A., Huang, S., Yang, Y. 2006. Predicting lodgepole pine site index from climatic parameters in Alberta. Forestry Chronicle, **82**: 562-571.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Government of Alberta, Pub. No. T/852.

Nigh, G.D., Ying, C.C., and Qian, H. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. Forest Science, **50**: 659-671.

Oliver, C.C., and Larson, B.C. 1996. Forest stand dynamics. John Wiley and Sons, New York, NY.

Sauchyn, D.J., Barrow, E.M., Hopkinson, R.F., and Leavitt, P.R. 2002. Aridity on the Canadian plains. Geographie Physique et Quaternaire, **56**: 247-259.

Sauchyn, D.J., and Skinner, W.R. 2001. A proxy record of drought severity for the southwestern Canadian Plains. Canadian Water Resources Journal, **26**: 253-272.

Sauchyn, D.J., Stroich, J., and Beriault, A. 2003. A paleoclimatic context for the drought of 1999-2001 in the northern Great Plains of North America. Geographical Journal, **169**: 158-167.

Schweingruber, F.H., Kairiukstis, L., and Shiyatov, S. 1990. Sample selection. *In* Methods of dendrochronology: Applications in the environmental sciences. *Edited by* E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 95-129.

Villalba, R., Veblen, T.T., and Ogden, J. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology, **75**: 1450-1462.

Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., and Aitken, S.N. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change biology, **12**: 2404-2416.

Woodward, F.I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge, UK.

Chapter II: Influences of climate on the radial growth of lodgepole pine in Alberta [1]

Introduction

The annual growth cycle of conifers alternates between phases of summer growth and winter dormancy in response to seasonal changes in climatic drivers of tree growth phenology (Havranek and Tranquillini 1995; Kramer et al. 2000; Green 2007). The seasonal periodicity of climatic effects on growth processes results in the formation of annual rings (Vaganov et al. 2006). Tree-ring analysis (dendrochronology) provides insight into the seasonal timing of growth-climate relationships (Fritts 1976; Vaganov et al. 2006). Dendrochronological techniques thus represent an alternative approach to examine tree growth phenology (Larcher 2003) integrated over greater time scales than short-term ecophysiology studies. Consideration of growth phenology parameters (e.g., bud-break heat sum requirements) has been shown to improve the predictive abilities of some climatically-sensitive forest growth models to accurately estimate the distribution of extant forests (Burton and Cumming 1995). Nonetheless, there is limited species-specific understanding of the climatic drivers of growth phenology for a number of tree species (Burton and Cumming 1995). Dendrochronology studies therefore can assist with the parameterization of climatically-sensitive forest growth models (Cook and Cole 1991; Loehle and LeBlanc 1996).

Most previous studies examining the influences of climate on the radial growth of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) have been

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conducted at a few locations (1-4 sites) and (or) of limited regional extent in the United States (Villalba et al. 1994; Sauchyn and Skinner 2001; Sauchyn et al. 2003; Case and Peterson 2007) and Canada (Sauchyn et al. 2002; Sauchyn et al. 2003). In contrast, the current study examined radial growth-climate relationships in lodgepole pine across a network of 17 sites in Alberta, covering a distance of 1100 km that separates the most distant sites. Dendrochronological methods were used to retrospectively identify the principal monthly and seasonal climatic factors that have influenced the historical, regional-scale pattern of radial growth of lodgepole pine in the cordilleran forests of Alberta over an 80-year period (1924-2003).

Materials and Methods

Site selection and field sampling

The 17 lodgepole pine sites included in this study (Table 2-1) were selected from the Alberta Forest Service permanent sample plot database (Alberta Land and Forest Service 1994). All sites were closed-canopied, even-aged stands of fire origin. The 17 sites covered the predominant latitudinal and elevational range of lodgepole pine in Alberta (Fig. 2-1). Stands were selected which showed no obvious recent history of disturbances (e.g., fire, disease, or insect damage). Most of the lodgepole pine stands were sampled from the main geographical range of lodgepole pine in Alberta, except for sites 6A and 6B which were sampled from a disjunct lodgepole pine population located in the western portion of the Cypress Hills Interprovincial Park (Fig. 2-1). At each site, an average of 21 dominant and co-dominant trees were sampled in a 50 m buffer zone surrounding each of the provincial government permanent sample plots (Table 2-2). Two

cores (at $\geq 90°$ to each other) were obtained per tree at breast height using an increment borer.

Sample processing

All tree cores were air dried, mounted on grooved boards, and sanded with progressively finer grades of sandpaper to highlight annual ring-width patterns (Stokes and Smiley 1996). All samples were visually crossdated under a binocular microscope to identify any missing and/or false rings (Yamaguchi 1991). For each core, annual ring width was measured using an image analysis system (DendroScan: Varem-Sanders and Campbell 1996). Images of increment cores were scanned in at an optical resolution of 1200 d.p.i. which corresponds to a measurement accuracy of 0.02 mm. This measurement accuracy was suitable for the majority of the samples since the overall average ring width was 1.24 mm (Table 2-2). Difficult sections of some increment cores containing extremely narrow rings were measured with a stage micrometer (Velmex: Bloomfield, New York) to an accuracy of 0.001 mm. The visual crossdating and tree-ring measurements were further verified via statistical crossdating with the program COFECHA from the Dendrochronology Program Library (Holmes 1992; Grissino-Mayer 2001).

Chronology development

Using the program ARSTAN (Holmes 1992), each ring-width series was detrended in three stages, first with a negative exponential curve, linear regression, or line through the mean resulting in low-frequency standardized (LFS) series. Detrending with

these conservative growth curves captures the strong juvenile growth period of pine as well as the trend of decreasing growth with age which is a reflection of the increasing geometric constraint of adding wood to a bole of increasing diameter. Before further detrending, LFS site chronologies were constructed by averaging the LFS series at each site.

For the second stage, each LFS series was detrended with a cubic-smoothing spline resulting in high-frequency standardized (HFS) series. A 50-year cubic-smoothing spline with a 50% frequency response was selected (Cook and Peters 1981). The characteristics of this spline preserve 99% of the variation in each ring-width series of each site at a wavelength of about 15 years. Consequently, common trends between trees at a site are preserved at the interannual to decadal time scales. A cubic spline captures growth releases and suppressions due to stand dynamics driven by competitive processes that are generally characteristic of closed-canopied forests. Before the next stage, HFS site chronologies were constructed by averaging the HFS series at each site.

For the third stage, autocorrelation in each HFS series was removed via autoregressive modeling resulting in high-frequency residual (HFR) series. Autoregressive modeling makes observations independent to meet the condition of most statistical analyses (Legendre and Legendre 1998). Autoregressive modeling removes low-frequency variation and enhances the common growth signal, which is usually better correlated with yearly climatic fluctuations. HFR site chronologies were constructed by averaging the HFR series at each site.

Radial growth-climate analyses

Climate data

Spatially interpolated climate data for each of the 17 lodgepole pine sites were provided by McKenney et al. (2001). McKenney et al. (2001) used the program ANUSPLIN (Hutchinson 2000) to conduct the spatial interpolations of climate variables based on thin-plate smoothing splines that are a function of site location (latitude, longitude, and elevation), and output of climate variables is provided at a spatial resolution of a 1 km (0.00833 degrees) grid. The primary climate variables provided included mean daily minimum and maximum temperature for each month and total monthly precipitation (PPT) and over the period of 1901-2003. Mean monthly temperature (TAV) was determined by averaging the mean daily minimum and maximum monthly temperatures.

Also considered were secondary climate variables derived from the primary ones including a Climate Moisture Index (Hogg 1997), monthly growing degree days above a base mean daily temperature of 5°C, and monthly chilling degree days below a base daily minimum temperature of 0°C (Brooks 1943). A suite of bioclimatic variables (e.g., minimum temperature of the coldest month, maximum temperature of the warmest month, etc.) were also considered (Houlder et al. 2000). According to exploratory correlation analyses, the response of radial growth to the secondary variables were either slightly stronger (Climate Moisture Index, growing degree days, chilling degree days) or appreciably weaker (bioclimatic variables) compared to the primary variables (PPT, TAV). Thus, since the secondary variables did not provide appreciably stronger insight

to the dendroclimatic relationships than what was already provided by the primary variables, the analysis with the secondary variables were not presented.

Site-level analyses

The relationships between the three chronology types (LFS, HFS, and HFR) at each site with each of the monthly climatic variables (TAV and PPT) were examined using Pearson correlation analyses. This was conducted over two growing seasons from April of the prior year (t-1) to October of the current year (t) (19 months). Since radial growth can respond more strongly with climate variables at the seasonal scale, correlation analysis was conducted to examine the relationship between the radial growth chronologies at each site with all possible seasonal (3 month periods) climate variables that cover the period of April (t-1) – October (t).

The radial growth-climate relationships were examined along a time period that corresponded with the well-replicated portion of the site chronologies which was determined using expressed population signal (EPS) analysis (Briffa and Jones 1990). An EPS $\geq$ 0.85 is considered a benchmark of optimal signal strength for a chronology. For sites 1A, 1B, and 1C, the start year (i.e., 1941, 1939, and 1960, respectively) for further analyses of radial growth-climate relationships was determined by the earliest year when there was a sufficient number of trees to reach an EPS $\geq$ 0.85 (Table 2-2). For all the other sites, the start year (i.e., 1924) for further analyses of radial growth-climate relationships was determined by the earliest year shared by all the sites when there was a sufficient number of trees to reach an EPS $\geq$ 0.85. The time frame for these radial growth-climate relationships were also used to calculate correlations between the site

chronologies. Principal component analysis was conducted on a correlation matrix of the 17 chronologies for each chronology type over the common period shared by all chronologies (i.e., 1960-2003). In principal component analysis, each year is considered a sample and each chronology a descriptor (Legendre and Legendre 1998). Principal component analysis reexpresses the original 17 chronologies into a few orthogonal variables that represent the main sources of variation. The program ARSTAN was used to compute all descriptive chronology statistics, including EPS and mean sensitivity (Table 2-2). Mean sensitivity provides a measure of the degree of high-frequency interannual variation in radial growth (Douglass 1920).

Regional-level analyses

Regional radial growth chronologies were constructed by averaging all of the 17 site chronologies for each chronology type (Fig. 2-2). Only segments of site chronologies with an EPS ≥ 0.85 were used to create the regional chronologies. The relationship of the regional chronologies and monthly and seasonal climatic variables was examined using correlation analysis. The climate data used in this analysis were combined (regionalized) climate data from all 17 sites. The regionalized-climate data were combined by first converting the raw climate data at each site into anomalies in °C (mean temperature) or mm (total precipitation) from their respective mean for the reference period of 1961-1990 (Jones and Hulme 1996). The climate variables of all 17 sites expressed as anomaly values were then averaged together to produce the regional climate variables.

Relationships between the regional chronologies and regional climate variables were also modeled using a step-wise multiple regression analysis, with forward selection, using the function *stepAIC* (package *MASS*) in the program R (R is the open-source version of S) (Venables and Ripley 2002). In addition to the monthly and 3 month seasonal scale; 2, 4, 5, and 6 month seasonal periods of the climate variables were also considered. Precipitation variables are in units of total mm for the monthly and seasonal periods. The regression model selected for each climate variable set (mean temperature and precipitation) and at each scale (monthly and seasonal (2, 3, 4, 5, and 6-month periods)) was selected based on minimizing the value of Akaike's information criterion as long as adding a predictor variable lowered the Akaike's information criterion value by a least 2 (Burnham and Anderson 2002). Akaike's information criterion penalizes models with too many parameters (Burnham and Anderson 2002). The climate variables which were used as the set of possible candidate predictor variables span a 19-month window covering two growing seasons from April of the prior year (t-1) to October of the current year (t) [apr(t-1)_oct(t)] over an 80 year period (1924-2003). For example, at the 6-month climate scale, there is a total of 14 possible candidate predictor variables: i.e., apr(t-1)_sep(t-1), may(t-1)_oct(t-1), jun(t-1)_nov(t-1), and so on, such that the remaining 11 variables are derived by shifting the start and end months of the preceding 6-month variable forward by one month. Since there is the potential for selecting seasonal climate variables with shared months, seasonal climate variables sharing the same month(s) as those seasonal variables selected earlier in the step-wise sequence were excluded from the regression model.

The candidate predictor variables for the final regression models consisted of the predictor variables selected for each climate scale. These candidate predictor variables were pooled together from across the climate scales and subjected to a final step-wise regression procedure in order to derive the final regression models. The final regression models for mean temperature and precipitation were each checked separately for multicollinearity between the predictor variables and none was present (all $p \geq 0.05$). The regression models were validated by comparing the error sum of squares (SSE) with the prediction sum of squares (PRESS) (Kutner et al. 2004) of each regression model. A PRESS value that is fairly close to a corresponding SSE value supports the validity of the regression model.

Not all terms of the final regression model for mean temperature could be combined with that of precipitation due to issues of multicollinearity between mean temperature and precipitation. For the study region, temperature and precipitation are generally inversely related throughout the year such that summers are generally both hot and dry and winters which are cold generally have high precipitation. Consequently, response function analysis was employed with the program PRECON using 999 bootstrap iterations (Fritts et al. 1991) in order to provide a better assessment of the relationship of radial growth with both mean temperature and precipitation (but only at the monthly scale since PRECON is limited to monthly climate data). Response function analysis is a form of multiple regression analysis in which the predictor variables are principal components of the climatic variables.

Results

Chronology characteristics

The regional LFS and HFS chronologies were used to highlight longer term (i.e., decadal) changes in radial growth, while the regional HFR chronology was used to explore dendroclimatic relationships at the regional-level. Over the time period after 1905 that was represented by at least half of the sites ($\geq$ 9 sites), the decadal trends captured by the 11-year Gaussian filter in the regional LFS and HFS chronologies (and to a lesser extent in the regional HFR chronology) indicated that there were pronounced periods of reduced radial growth in the 1910s to mid 1920s and the mid 1940s till the 1950s (Fig. 2-2). There were also periods of reduced radial growth from the mid 1980s till the 1990s.

The HFR site chronologies demonstrated a stronger common radial growth signal as indicated first by a higher mean correlation between sites of $r = 0.36$ than for either the HFS (0.30) and LFS (0.18) chronologies. Furthermore, although the three chronology types had a similar response pattern to the climate variables, the relationships were strongest with the HFR chronologies. Consequently, only the HFR site chronologies and regional chronology, and their response to climate, are described further (Table 2-2). An average sample size of 9 trees was sufficient to achieve an EPS value of 0.85. Principal component analysis of the HFR site chronologies showed that only the percentage of the total variance explained by the first principal component (50.4%) was greater than that expected under the broken stick null model (20.2%) and therefore is considered the only meaningful principal component to interpret (Frontier 1976; Legendre and Legendre 1998) (Fig. 2-3a). The 17 site chronologies have the same sign and similar magnitude of

their loadings onto the first principal component (Fig. 2-3b). The similar chronology loadings onto the first principal component suggests that growth at the 17 sites are similarly affected by an external environmental forcing (i.e., climate), and it is on this basis that it can be explicitly justified to combine the individual site chronologies into a single regional chronology and explore growth-climate relationships at the regional scale.

Radial growth-climate relationships

Site-level

In terms of monthly temperature, the HFR site chronologies were most often negatively associated with August mean temperature of the previous year (August (t-1)) with a mean correlation coefficient (r) of -0.30 (Fig. 2-4a). Similarly, in terms of monthly precipitation, the site chronologies were most frequently positively correlated with August (t-1) precipitation (mean r = 0.29) (Fig. 2-4b).

At the seasonal scale, radial growth responded negatively to 3-month mean temperature ending in September (t-1) (Fig. 2-5a) but the frequency and strength of this relationship (mean r = -0.25) was not better than with monthly August (t-1) mean temperature (Fig. 2-4a). Seasonalizing mean temperature did however improve the correlation of radial growth to winter conditions, most notably the frequent, positive relationship with 3-month mean temperature ending in January (t) (mean r = 0.24). The frequency and strength with which the site chronologies responded to 3-month precipitation amounts ending in October (t-1) (mean r = 0.25) (Fig. 2-5b) was lower than with monthly August (t-1) precipitation (Fig. 2-4b). Seasonalizing precipitation did,

however, slightly increase the frequency and strength with which the site chronologies responded to 3-month precipitation amounts ending in March (t) (mean r = -0.16).

Regional-level

In addition to the significant negative relationship between the regional HFR chronology and regional mean monthly temperature in August (t-1) (which was revealed at the site-level) there were also significant positive correlations with November (t-1), January (t), March (t), April (t), and October (t) mean temperature (Fig. 2-6a). Regional radial growth was not only positively correlated with August (t-1) precipitation (which was revealed at the site-level), but was also negatively associated with March (t) precipitation.

Seasonalizing the mean temperature climate variables showed significant negative correlations between regional radial growth and 3-month mean temperature ending in either August (t-1) or September (t-1) (Fig. 2-6b). Warmer winters appeared to promote better radial growth in the following growing season; see the positive correlations between radial growth and 3-month mean temperatures ending in December (t-1) through May (t). There were also positive correlations between radial growth and 3-month mean temperatures ending in September (t) or October (t). Radial growth was positively correlated with the amount of precipitation for the 3-month period ending in September (t-1) or October (t-1), and was negatively correlated with precipitation ending in March (t).

The most parsimonious regression model for each set of climate variables (TAV, PPT, or TAV + PPT) that explained the most variance in regional radial growth are

provided in Table 2-3. The prediction sum of squares (PRESS) were reasonably close to the error sum of squares (SSE) which lends support to the validity of the regression models (Kutner et al. 2004) (Table 2-3). The strongest relationship ($R^2 = 0.418$) was obtained with the regression model that included monthly August (t-1) and September (t-1) mean temperature and mean temperature for the 6 months from November (t-1) to April (t). Other regression models were weaker; for precipitation (PPT, $R^2 = 0.174$) and for temperature and precipitation (TAV + PPT, $R^2 = 0.256$). The regression model for precipitation could not be completely combined with that of temperature because of multicollinearity between the amount of precipitation for the 2-month period of August (t-1) to September (t-1) and either monthly August (t-1) ($r = -0.41$, $p < 0.00014$) or September (t-1) ($r = -0.48$, $p < 0.0001$) mean temperature. Multicollinearity was also present between mean temperature for the 6-month period from November (t-1) to April (t) and the amount of precipitation for the 2-months from February (t) to March (t) ($r = -0.40$, $p < 0.00020$). The response function model of both mean temperature and precipitation explained 61.6% of the variation in radial growth (Fig. 2-7). Significant response function coefficients occurred in August (t-1), September (t-1), November (t-1), February (t), and April (t) for mean temperature and in August (t-1) and March (t) for precipitation. The observed regional radial growth versus modeled radial growth for mean temperature and for the response function model are presented in Fig. 2-8.

Discussion

Results indicated that lodgepole pine radial growth was strongly conditioned by heat and moisture stress in late summer of the previous year (t-1) since radial growth was negatively related to late summer temperature and positively associated with late summer precipitation. These lagged climate variables were also important drivers in the regression and response function models predicting regional-scale radial growth (Table 2-3; Fig. 2-7). Lags in response to climatic stresses in northern pines (Villalba et al. 1994; Case and MacDonald 1995; Case and Peterson 2007) and spruces (St. George and Luckman 2001; Chhin et al. 2004) occur partly because climatic conditions in late summer in the year of bud formation generally affects the size of the buds and the number of leaf primordia produced within them (O'Reilly and Owens 1987; Kozlowski et al. 1991; Owens 2006). The size of the dormant bud then affects the amount of leaf area for the most photosynthetically efficient class of needles produced in the year of bud expansion and ring formation. Secondly, in late summer, favourable climatic conditions lead to the build up of carbohydrate reserves (Landhäusser and Lieffers 2003) which can be used to drive radial growth the following growing season (Kozlowski et al. 1991). Furthermore, high temperatures in late summer are associated with increased rates of respiration which in turn can reduce carbohydrate reserves (Kozlowski et al. 1991). The results of this study indirectly suggests that heat and/or moisture stress (either directly due to low precipitation or indirectly by temperature-induced drought stress (Barber et al. 2000)) affect the build-up of storage reserves and next year's development of foliage. Other studies have shown that lodgepole pine is sensitive to moisture stress (Sauchyn and Skinner 2001; Sauchyn et al. 2002; Sauchyn et al. 2003; Case and Peterson 2007).

In this study, lodgepole pine radial growth was greater following warm winters, which is consistent with other studies of lodgepole pine (Villalba et al. 1994). Radial growth was also greater following winters with low precipitation. There are a number of possible ecophysiological mechanisms whereby conditions during winter can affect tree growth (Havranek and Tranquillini 1995): (1) The overwintering dormant buds are considered to be susceptible to damage by ice formation within the buds because of cold winters (Woodward 1995). (2) Wind and snow abrasion during winter can damage tree crowns, leading to foliage loss (Grier 1988) and the damaged cuticle of needles can lead to excessive water loss during times of frozen soil (Havranek and Tranquillini 1995). "Red belt" in lodgepole pine is generally caused by extremely cold weather followed by drying Chinook winds (Lotan and Critchfield 1990). This type of winter desiccation injury influences the latitudinal and altitudinal distribution of conifers in North America (Kozlowski et al. 1991). (3) Cold winter conditions also increase the risk and severity of xylem cavitation (Sperry and Robson 2001; Pittermann and Sperry 2006). When xylem water freezes, dissolved gases are released which form bubbles that can lead to blockage of the xylem and a restriction in water transport to foliage. The ability to recover from freeze-induced cavitation affects growth the following growing season (Woodward 1995), and cavitation has been implicated as a possible cause of some forest declines (Auclair et al. 1992; Bourque et al. 2005). (4) The start of the growing season may be delayed by two factors associated with winters: Cold winter temperatures will usually result in a greater depth of soil freezing. Second, high snowfall will take more time to melt in the spring. Both factors contribute to delays in soil heating (Euskirchen et al.

2006). However, patterns in the extent of frozen soil are complicated by the timing of and insulating effects of snow.

Radial growth of lodgepole pine was apparently affected by the length of the current growing season, based on the positive correlations between radial growth and 3-month mean temperatures ending in May (t) and October (t) (Fig. 2-6a), and the negative relationship with 3-month precipitation ending in March (t) (Fig. 2-6b). Low precipitation in late winter/early spring and warm springs contribute to earlier snowmelt and soil warming, leading to an earlier start to the growing season. Similarly, lodgepole pine radial growth at high elevations in the North Cascades of Washington was negatively affected by high spring snow depth (Case and Peterson 2007). Warm temperatures in late fall should also prolong the growing season for lodgepole pine radial growth. The positive response to fall temperature in October of the current growing season is consistent with other studies of lodgepole pine (Villalba et al. 1994). Although the latest date for diameter growth cessation was in mid-September for provenances of lodgepole pine in British Columbia and the Yukon (O'Reilly and Owens 1989), the results of this study suggest that cambial growth can continue until October, when photosynthesis still occurs in some boreal conifers (Man and Lieffers 1997).

While some aspects of the radial growth-climate relationships of lodgepole pine were consistent with other previous studies of lodgepole pine (Villalba et al. 1994; Sauchyn and Skinner 2001; Sauchyn et al. 2002; Sauchyn et al. 2003; Case and Peterson 2007) and other conifers in mountainous areas (St. George and Luckman 2001), there are also some notable differences. For instance, in the subalpine (Villalba et al. 1994) and tree-line (St. George and Luckman 2001) zones of mountainous environments, tree radial

growth was generally limited by cool temperature conditions of the current growing season. Also, temperature limits the distribution of conifers in high elevation sites where the 10°C July-isotherm corresponds well with the position of the alpine timberline (Tranquillini 1979; Grace 1989). In this study, radial growth was not significantly correlated with the individual summer months or seasonal periods that only included the summer months in the current growing season for the regional-scale analysis (Fig. 2-6). Furthermore, there were no significant response function coefficients for the summer months in the current growing season (Fig. 2-7). The lack of a positive response to summer temperature can be a indication that most of the sites selected in the current study are from lower elevational zones compared to the subalpine (Villalba et al. 1994) and tree-line (St. George and Luckman 2001) sites examined in other studies. Therefore, the lack of a positive response to temperature conditions during the current growing season suggests that the heat requirements for lodgepole pine radial growth were easily met at these lower elevations. In fact, lodgepole pine generally had the opposite problem faced by tree-line trees in that radial growth was negatively affected by excess heat in the prior growing season.

It was observed that for most of the sites in this study and thus captured at the regional-scale, lodgepole pine was positively correlated with prior year summer precipitation and negatively correlated with prior year summer temperature. In contrast, Villalba et al. (1994) only observed a negative correlation with prior year August temperature. This may be a reflection that the four sites selected in their study may not be moisture stressed. The seasonal timing of the radial growth-climate relationships was also different. Lodgepole pine in this study took advantage of the prolonged growing

season in the year of ring formation characterized by warm springs with little precipitation and warm falls. While Villalba et al. (1994) also observed that warm fall temperatures also prolonged the growing season in the year of ring formation, they also observed that lodgepole pine was very responsive to conditions that prolonged the growing season into the fall of the prior year. These conditions included warm fall temperatures and low fall precipitation. These differences in the seasonal timing of dendroclimatic relationships can reflect different patterns in growth phenology and climatic regimes between the study area of this study and that of the more southerly sites examined by Villalba et al. (1994) in the Colorado Front Range (40°N).

The main objective of Sauchyn et al. (2003) in relating lodgepole pine radial growth to precipitation in the Cypress Hills was to extend the record of summer precipitation before the instrumental record using lodgepole radial growth as a climate proxy. In a related study, Sauchyn et al. (2002) applied tree-ring analysis of lodgepole pine in the Cypress Hills towards the reconstruction of a summer aridity index defined as the ratio of precipitation to potential evapotranspiration, and potential evapotranspiration was determined as a function of mean air temperature. Radial growth was more strongly correlated with precipitation compared to the negative relationship with potential evapotranspiration (Sauchyn et al. 2002). In the present study, while the sites in the western Cypress Hills also responded to summer moisture stress in the current and previous year (Fig. 2-4b), this study underscored the role that negative relationships with summer and fall temperature play in indirectly inducing moisture stress (Fig. 2-4a).

References

Alberta Land and Forest Service. 1994. Permanent sample plot field procedures manual. Timber Management Branch, Alberta Forest Service, Edmonton, Alberta. Pub. FMOPC 83-03.

Auclair, A.N.D., Worrest, R.C., Lachance, D., and Martin, H.C. 1992. Climatic perturbation as a general mechanism of forest dieback. *In* Forest decline concepts. *Edited by* P.D. Manion and D. Lachance. The American Phytopathological Society, St. Paul, MN. pp. 38-58.

Barber, V. A., Juday, G.P., and Finney, B.P. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature, **405**: 668-73.

Bourque, C.P.A., Cox, R.M., Allen, D.J., Arp, P.A., and Meng, F.R. 2005. Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. Global Change Biology, **11**: 1477-1492.

Briffa, K., and Jones, P.D. 1990. Basic chronology statistics and assessment. *In* Methods of Dendrochronology. *Edited by* E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Boston, MA. pp. 137-152.

Brooks, C.E.P. 1943. Interpolation tables for daily values of meteorological elements. Quarterly Journal Royal Meteorological Society, **69**: 160-162.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Burton, P.J., and Cumming, S.G. 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air and Soil Pollution, **82**: 401-414.

Case, M.J., and Peterson, D.L. 2007. Growth-climate relations of lodgepole pine in the North Cascades National Park, Washington. Northwest Science, **81**: 62-75.

Case, R.A., and MacDonald, G.M. 1995. A dendroclimatic reconstruction of annual precipitation on the western Canadian Prairies since A.D. 1505 from *Pinus flexilis* James. Quaternary Research, **44**: 267-275.

Chhin S., Wang, G.G., and Tardif, J. 2004. Dendroclimatic analysis of white spruce at its southern limit of distribution in the Spruce Woods Provincial Park, Manitoba, Canada. Tree-Ring Research, **60**: 31-43.

Cook, E.R., and Cole, J. 1991. On predicting the response of forests in eastern North America to future climate change. Climatic Change, **19**: 271-282.

Cook, E.R., and Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin, **41**: 45-53.

Douglass, A.E. 1920. Evidence of climatic effects in the annual rings of trees. Ecology, **1**: 24-32.

Euskirchen, E.S., McGuire, A.D., Kicklighter, D.W., Zhuang, Q., Clein, J.S., Dargaville, R.J., Dye, D.G., Kimball, J.S., McDonald, K.C., Melillo, J.M., Romanovsky, V.E., and Smith, N.V. 2006. Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. Global Change Biology, **12**: 731-750.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, UK.

Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V., and Shashkin, A.V. 1991. Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell-size, cell-wall thickness and wood density. Climate Research, **1**: 97-116.

Frontier, S. 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle du baton brisé. Journal of Experimental Marine Biology and Ecology, **25**: 67-75.

Grace, J. 1989. Tree lines. Philosophical Transactions of the Royal Society of London, **B324**: 233-245.

Green, D.S. 2007. Controls of growth phenology vary in seedlings of three, co-occurring ecologically distinct northern conifers. Tree Physiology, **27**: 1197-1205.

Grier, C.C. 1988. Foliage loss due to snow, wind, and winter drying damage: its effects on leaf biomass of some western conifer forests. Canadian Journal of Forest Research, **18**: 1097-1102.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research, **57**: 205-221.

Havranek, W.M., and Tranquillini, W. 1995. Physiological processes during winter dormancy and their ecological significance. *In* Ecophysiology of coniferous forests. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 95-124.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology, **84**: 115-122.

Holmes, R.L., 1992. Dendrochronology program library. Laboratory of Tree-Ring Research, University of Arizona, Tuscon, Version 1992-1.

Houlder, D., Hutchinson, M., Nix, H., and McMahon, J. 2000. ANUCLIM 5.1 User's Guide. Centre for Resource and Environmental Studies, Australian National University, Canberra ACT 0200, Australia.

Huang, S., Morgan, D.J., Klappstein, G., Heidt, J., Yang, Y., and Greidanus, G. 2001. Yield tables for seed-origin natural and regenerated lodgepole pine stands. Alberta Sustainable Resource Development, Edmonton, Alberta. Tech. Rep. Pub. No. T/485.

Hutchinson, M.F. 2000. ANUSPLIN Version 4.1 User Guide. Centre for Resource and Environmental Studies, Australian National University, Canberra ACT 0200, Australia.

Jones, P.D., and Hulme, M. 1996. Calculating regional climatic time series for temperature and precipitation: methods and illustrations. International Journal of Climatology, **16**: 361-377.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.

Kramer, K., Leinonen, I., and Loustau, D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperature and Medtirranean forests ecosystems: an overview. International Journal of Biometeorology, **44**: 67-75

Kutner, M.H., Nachtsheim, C.J., Neter, J., and Li, W. 2004. Applied linear statistical models. 5th ed. McGraw-Hill, New York, NY.

Landhäusser, S.M., and Lieffers, V.J. 2003. Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. Trees, **17**: 471-476.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 4th ed. Springer, Berlin.

Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd ed. Developments in Environmental Modeling 20, Elsevier Science B.V., Amsterdam.

Loehle, C., and LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling, **90**: 1-31.

Lotan, J.E., and Critchfield, W.B. 1990. *Pinus contorta* Dougl. Ex. Loud. or Lodgepole pine. *In* Silvics of North America: 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv., Washington, DC. Agric. Handbook 654. pp. 302-315

Man, R., and Lieffers, V.J. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiology, **17**: 437-444.

McKenney, D.W., Hutchinson, M.F., Kesteven, J., and Venier, L. 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Canadian Journal of Plant Science, **81**: 129-143

Owens, J.N. 2006. Reproductive biology of lodgepole pine. Forest Genetics Council (FGC) of British Columbia. Extension Note 07.

O'Reilly, C., and Owens, J.N. 1987. Long-shoot bud development, shoot growth, and foliage production in provenances of lodgepole pine. Canadian Journal of Forest Research, **17**: 1421-1433.

O'Reilly, C., and Owens, J.N. 1989. Shoot, needle, and cambial growth phenology and branch tracheid dimensions in provenances of lodgepole pine. Canadian Journal of Forest Research, **19**: 599-605.

Pittermann, J., and Sperry, J.S. 2006. Analysis of freeze-thaw embolism in conifers: the interaction between cavitation pressure and tracheid size. Plant Physiology, **140**: 374-382.

Sauchyn, D.J., Barrow, E.M., Hopkinson, R.F., and Leavitt, P.R. 2002. Aridity on the Canadian plains. Geographie Physique et Quaternaire, **56**: 247-259.

Sauchyn, D.J., and Skinner, W.R. 2001. A proxy record of drought severity for the southwestern Canadian Plains. Canadian Water Resources Journal, **26**: 253-272.

Sauchyn, D.J., Stroich, J., and Beriault, A. 2003. A paleoclimatic context for the drought of 1999-2001 in the northern Great Plains of North America. The Geographical Journal, **169**: 158-167.

Sperry, J.S., and Robson, D.G. 2001. Xylem cavitation and freezing in conifers. *In* Conifer Cold Hardiness. *Edited by* S. Colombo and F. Bigras. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 121-136.

St. George, S., and Luckman, B.H. 2001. Extracting a paleotemperature record from *Picea engelmanni* tree-line sites in the central Canadian Rockies. Canadian Journal of Forest Research, **31**: 457-470.

Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. The University of Arizona Press, Tuscon.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Springer-Verlag, Berlin, Germany.

U.S. Geological Survey. 1999. Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. [online]. U.S. Geological Survey, Reston, VA. Available from http://esp.cr.usgs.gov/data/atlas/little/index.html [accessed 2007 January 10].

Vaganov, E.A., Hughes, M.K., and Shashkin, A.V. 2006. Growth dynamics of conifer tree rings: images of past and future environments. Ecological Studies 183, Springer-Verlag, Berlin.

Varem-Sanders, T.M.L., and Campbell, I.D. 1996. DendroScan: a tree-ring width and density measurement system. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta. Spec. Rep. 10.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York, NY.

Villalba, R., Veblen, T.T., and Ogden, J. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology, **75**: 1450-1462.

Woodward, F.I. 1995. Ecophysiological controls of conifer distributions. *In* Ecophysiology of coniferous forests. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 79-94.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research, **21**: 414-416.

Table 2-1. Characteristics of the 17 lodgepole pine study sites.

Site	ER[1]	Elev. (m)	Latitude	Longitude	Aspect	Slope (°)	TAV[2] (°C)	PPT[2] (mm)	Age[3] (yr)	DBH[4] (cm)
1A	HL	1022	56°39'N	119°2'W	N	2	-1.68	489	61 ± 4	22.5 ± 2.8
1B	HL	1011	56°38'N	119°2'W	SW	3	-1.61	487	63 ± 3	23.5 ± 2.3
1C	HL	745	57°18'N	119°57'W	W	2	-0.82	448	43 ± 1	23.5 ± 2.3
2A	FH	1147	54°4'N	117°8'W	W	13	1.16	568	93 ± 6	31.8 ± 4.4
2B	FH	1070	54°6'N	116°59'W	S	3	1.40	559	95 ± 7	28.0 ± 3.8
2C	FH	924	54°8'N	116°45'W	-	0	1.89	542	113 ± 8	32.2 ± 4.2
3A	FH	1673	52°41'N	116°25'W	W	34	-0.42	662	92 ± 5	15.3 ± 2.1
3B	FH	1233	53°3'N	115°57'W	-	0	1.12	581	98 ± 3	27.6 ± 2.8
3C	FH	906	53°10'N	115°18'W	W	2	2.24	546	90 ± 3	28.1 ± 2.4
4A	FH	1718	52°4'N	115°29'W	N	2	-0.31	648	96 ± 4	19.2 ± 1.3
4B	FH	1532	52°9'N	115°27'W	W	38	0.58	614	88 ± 4	22.5 ± 3.2
4C	FH	1119	52°19'N	115°14'W	-	0	2.41	559	98 ± 4	28.7 ± 3.0
5A	RM	1773	50°15'N	114°35'W	W	10	0.65	706	123 ± 5	15.2 ± 1.5
5B	RM	1735	49°45'N	114°29'W	S	15	1.27	745	80 ± 3	17.7 ± 1.5
5C	RM	1649	50°3'N	114°26'W	E	4	1.47	674	78 ± 3	22.7 ± 2.3
6A	CH	1458	49°37'N	110°20'W	SW	8	1.81	436	103 ± 8	30.7 ± 5.8
6B	CH	1307	49°41'N	110°10'W	NE	5	2.31	409	117 ± 7	37.9 ± 5.2

[1] ER, elevational region abbreviations: HL, Boreal Highlands; FH, Foothills; RM, Rocky Mountains; CH, Cypress Hills

[2] Climate variable abbreviations: TAV, mean annual temperature; PPT, total annual precipitation. Climate variables determined for annual period of January-December from 1961-1990.

[3] Average age at coring height (± 1 SD)

[4] Average diameter at breast height (± 1 SD)

Table 2-2. Characteristics of tree-ring chronologies.

Site	Interval	Total trees (radii)	Mean ring width (mm)	Absent rings (%)	MS[1]	r_{ac}[2]	r_{bt}[3]	EPS[4]	EPS ≥ 0.85 Year (trees)[5]
1A	1938-2004	18 (32)	1.58	0.20	0.17	-0.11	0.39	0.92	*1941 (9)
1B	1937-2004	20 (34)	1.60	0.05	0.15	-0.02	0.37	0.92	*1939 (10)
1C	1959-2004	20 (36)	2.28	0.00	0.21	0.04	0.46	0.94	*1960 (7)
2A	1901-2004	19 (32)	1.46	0.00	0.14	0.01	0.45	0.94	1905 (7)
2B	1900-2004	19 (34)	1.23	0.00	0.14	0.03	0.36	0.91	1905 (11)
2C	1874-2004	19 (34)	1.20	0.05	0.17	-0.06	0.36	0.91	1888 (11)
3A	1906-2003	19 (34)	0.70	0.03	0.16	-0.06	0.48	0.95	1906 (7)
3B	1899-2003	20 (36)	1.20	0.06	0.14	0.00	0.36	0.92	1904 (11)
3C	1908-2003	18 (31)	1.30	0.14	0.17	0.01	0.35	0.90	1912 (11)
4A	1900-2003	19 (34)	0.84	0.03	0.15	0.08	0.48	0.95	1902 (7)
4B	1906-2003	20 (35)	1.10	0.00	0.14	-0.11	0.49	0.94	1910 (7)
4C	1900-2003	20 (34)	1.25	0.21	0.17	0.04	0.42	0.93	1902 (8)
5A	1874-2004	20 (40)	0.53	0.04	0.15	0.12	0.47	0.94	1876 (7)
5B	1920-2004	17 (27)	0.98	0.00	0.14	0.04	0.37	0.91	1923 (10)
5C	1922-2004	19 (35)	1.21	0.07	0.14	0.08	0.43	0.93	†1924 (8)
6A	1874-2003	38 (68)	1.22	0.06	0.15	0.08	0.40	0.96	1893 (9)
6B	1873-2003	38 (74)	1.34	0.56	0.23	-0.03	0.46	0.97	1874 (7)
Mean	99 years	21 (38)	1.24	0.09	0.16	0.01	0.42	0.93	1910 (9)

[1] MS (mean sensitivity) of each HFR chronology

[2] r_{ac} (autocorrelation coefficient) measures the correlation of each HFR chronology with itself at a lag of 1 year

[3] r_{bt} (between-tree correlation) based on the HFR chronologies

[4] EPS (expressed population signal) based on the HFR chronologies

[5] The earliest date and number of trees to reach an EPS ≥ 0.85

* For each site in sampling zone 1, the start year for further analyses of growth-climate relationships is determined by the earliest year that has an EPS ≥ 0.85

† For all the remaining sites in sampling zones 2-6, the start year (i.e., 1924) for further analyses of growth-climate relationships is determined by the earliest year shared by all the sites which has an EPS ≥ 0.85

Table 2-3. Regression models relating the regional-scale radial growth index (RGI) based on the HFR chronology (Fig. 2-2c) with key climate variables.

Climate variable set	Regression model	Adj. R^2	RMSE	SSE	PRESS
TAV	RGI = 0.993 – 0.03045 [T1_aug(t-1)] – 0.01102 [T1_sep(t-1)] + 0.02114 [T6_nov(t-1)_apr(t)]	0.418	0.0667	0.338	0.379
PPT	RGI = 1.008 + 0.00090 [P2_aug(t-1)_sep(t-1)] – 0.00117 [P2_feb(t)_mar(t)]	0.174	0.0794	0.486	0.524
TAV + PPT	RGI = 1.005 + 0.00081 [P2_aug(t-1)_sep(t-1)] + 0.01596 [T6_nov(t-1)_apr(t)]	0.256	0.0754	0.438	0.470

Note: Regression models were built from either mean temperature (TAV), precipitation (PPT), or a combination of TAV and PPT; the regression model based on TAV is plotted as thin lines in Fig. 2-8a. The variable T1_aug(t-1) is August mean temperature of the previous year (t-1); T1_sep(t-1) is September (t-1) mean temperature; [T6_nov(t-1)_apr(t)] is 6-month mean temperature for the period of November (t-1) to April of the current year (t); P2_aug(t-1)_sep(t-1) is 2-month precipitation amounts from August (t-1) to September (t-1); and P2_feb(t)_mar(t) is 2-month precipitation amounts from February (t) to March (t). Regional climate variables are expressed as anomalies in °C (TAV) or mm (PPT) from the reference period of 1961-1990. Other abbreviations: RMSE, root mean squared error; SSE, error sum of squares; PRESS, prediction sum of squares (Kutner et al. 2004).

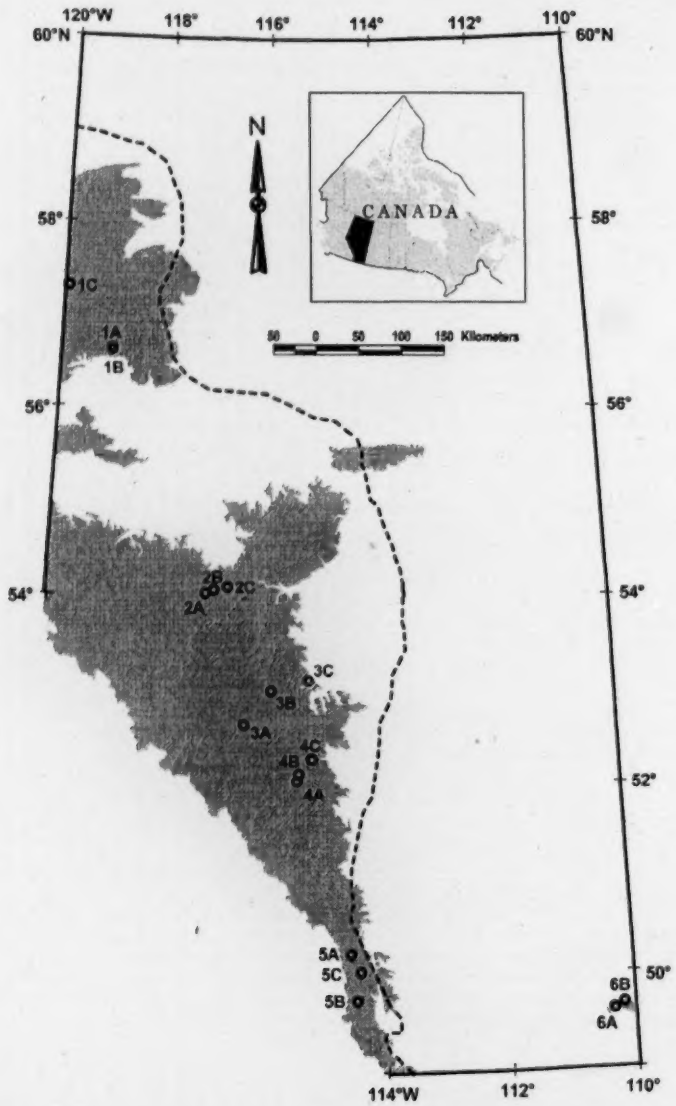


Figure 2-1. Distribution of the 17 lodgepole pine sites in the cordilleran forests of Alberta (shaded grey). West of the dashed line is the main geographic range of lodgepole pine in Alberta (U.S. Geological Survey 1999).

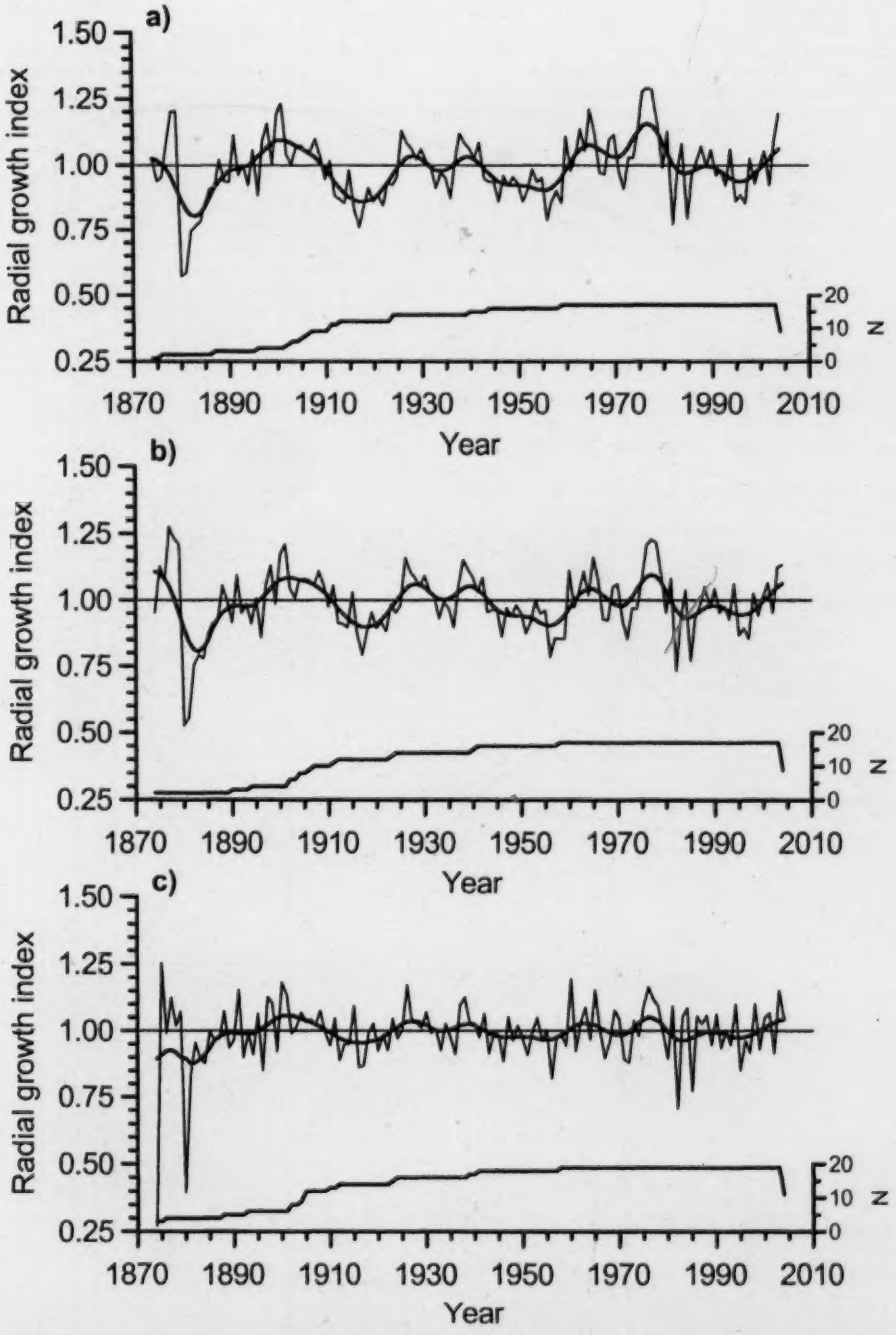


Figure 2-2. The regional radial growth chronology of the 17 lodgepole pine sites combined for each of three chronology types: (a) low-frequency standard chronology, (b) high-frequency standard chronology, and (c) high-frequency residual chronology. The bold line is a 11-yr Gaussian filter, and N is the number of sites with trees contributing to the analysis.

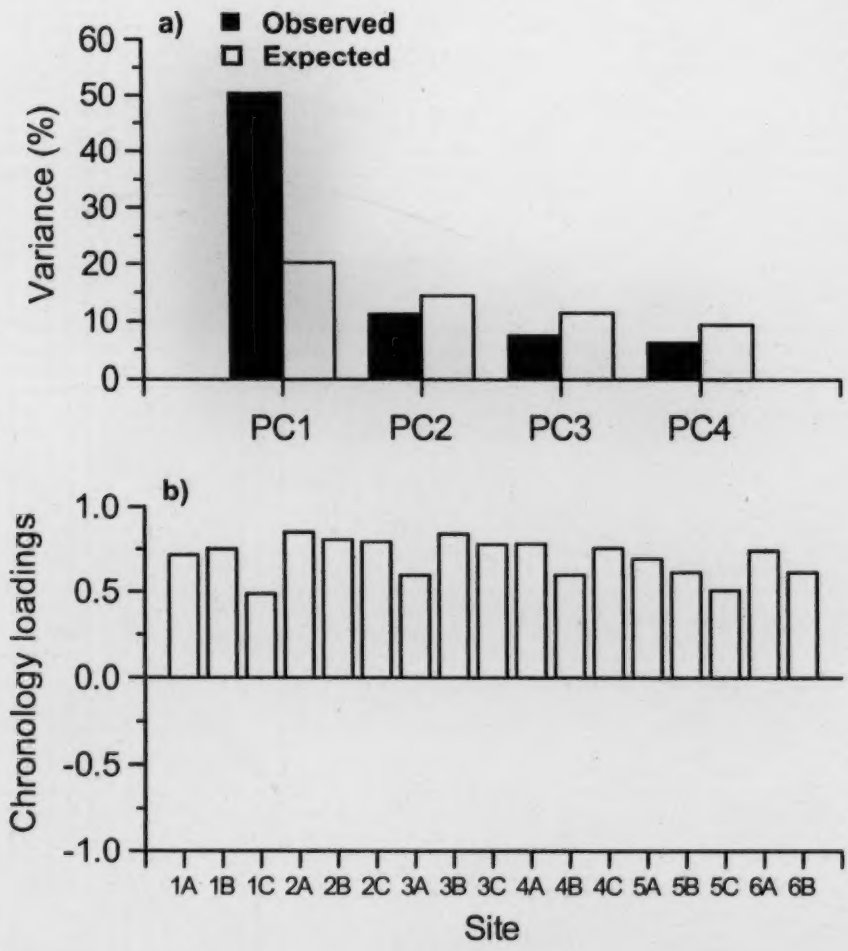
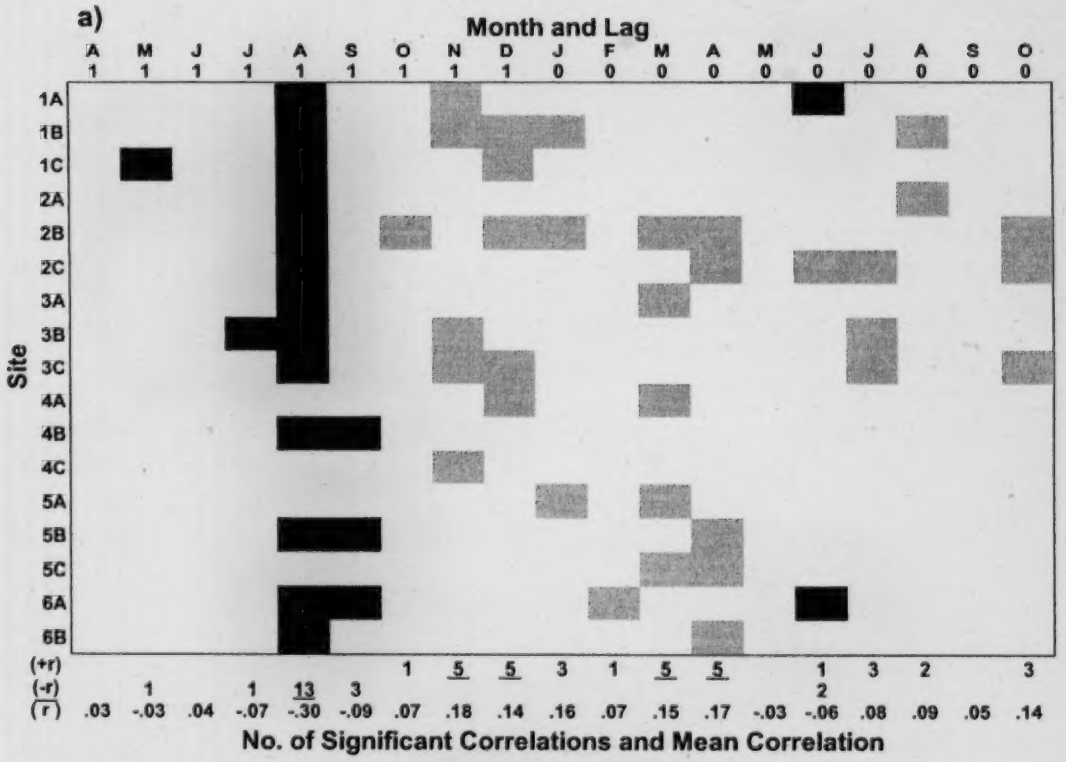
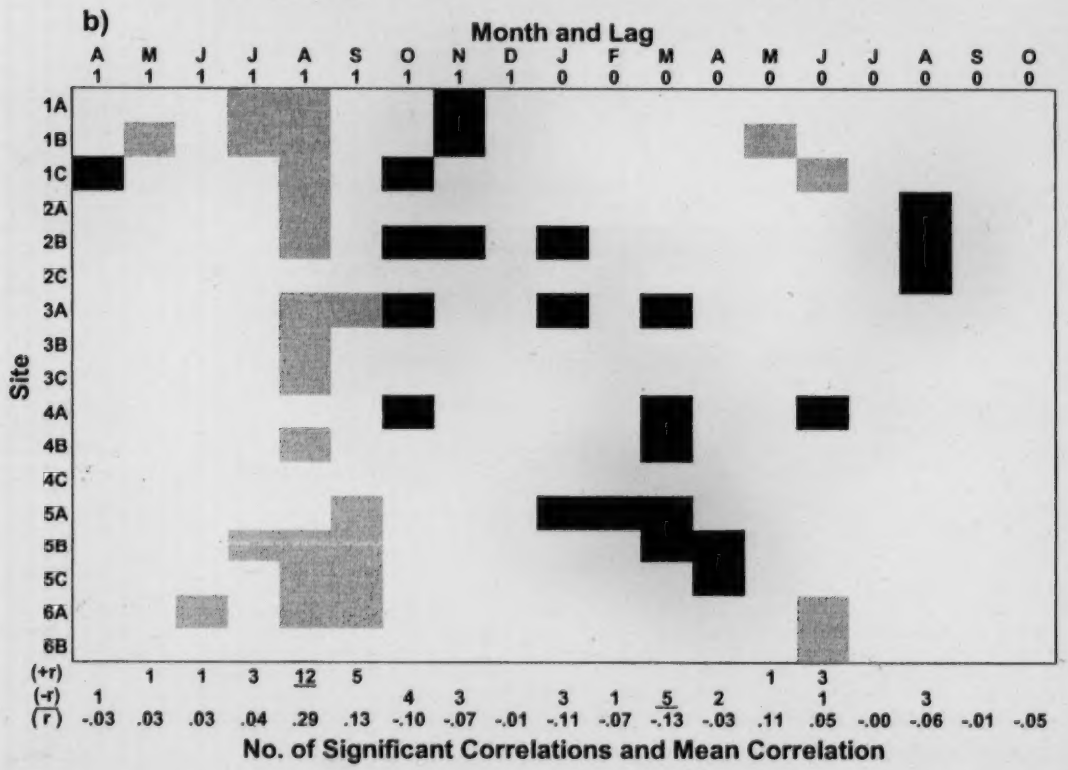


Figure 2-3. Principal component analysis of the high-frequency residual chronologies of the 17 lodgepole pine sites: (a) Percentage of the observed total variance explained by each of the first four principal components (PC1-PC4) compared to the expected values from the broken stick null model (Frontier 1976; Legendre and Legendre 1998). (b) The loadings of each of the 17 site chronologies onto PC1.


a)
Month and Lag
A M J J A S O N D J F M A M J J A S O
1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0
1A
1B
1C
2A
2B
2C
3A
3B
3C
4A
4B
4C
5A
5B
5C
6A
6B
Site
(+r) 1 5 5 3 1 5 5 1 3 2 3
(-r) 1 1 13 3 2
(r̄) .03 -.03 .04 -.07 -.30 -.09 .07 .18 .14 .16 .07 .15 .17 -.03 -.06 .08 .09 .05 .14
No. of Significant Correlations and Mean Correlation

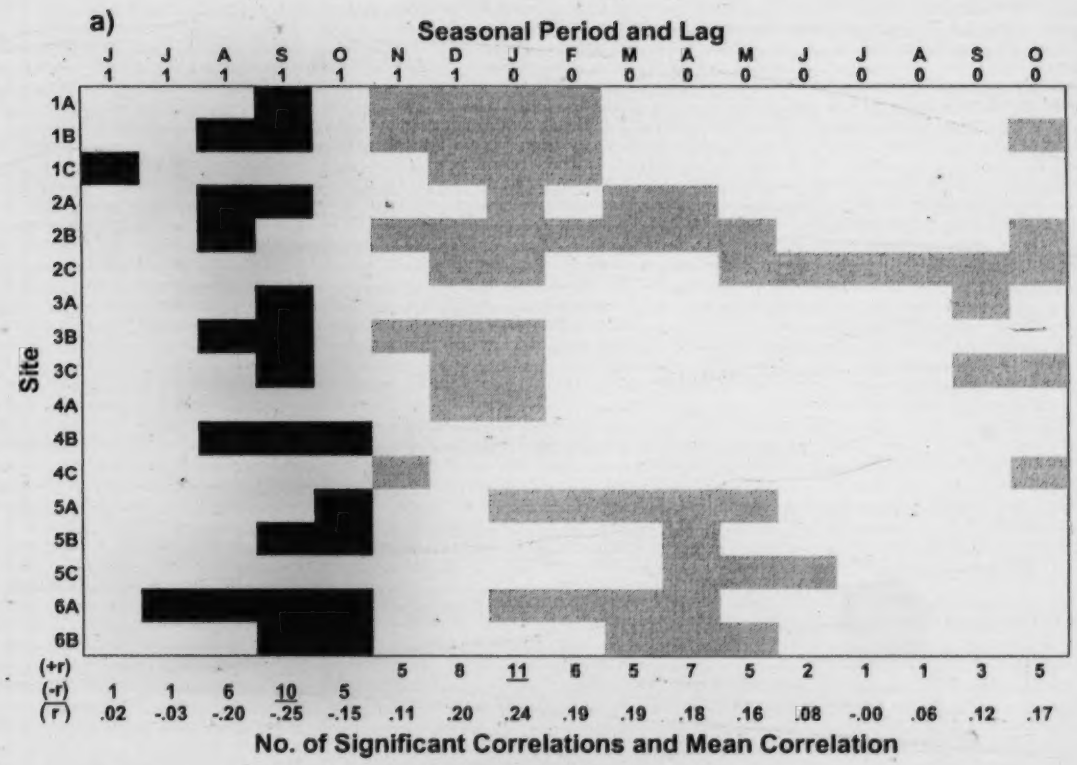

b)
Month and Lag
A M J J A S O N D J F M A M J J A S O
1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0
1A
1B
1C
2A
2B
2C
3A
3B
3C
4A
4B
4C
5A
5B
5C
6A
6B
Site
(+r) 1 1 3 12 5 1 3
(-r) 1 4 3 3 1 5 2 1 3
(r̄) -.03 .03 .03 .04 .29 .13 -.10 -.07 -.01 -.11 -.07 -.13 -.03 .11 .05 -.00 -.06 -.01 -.05
No. of Significant Correlations and Mean Correlation

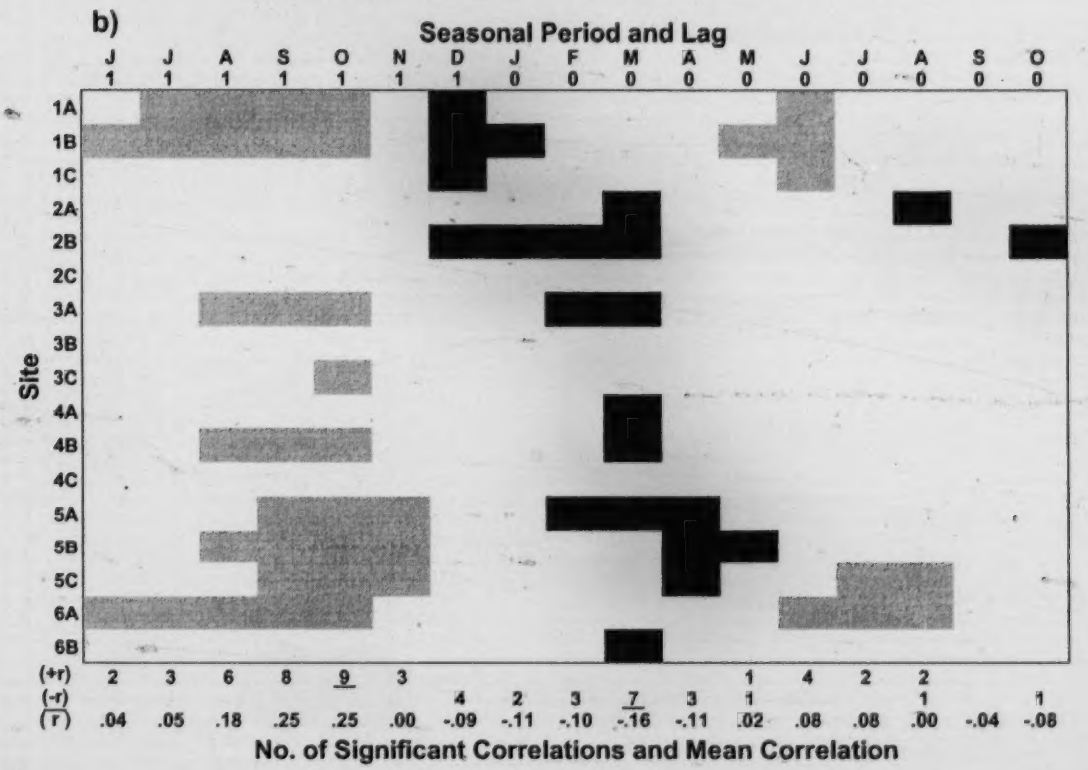
(Note: Caption for previous figure)

Figure 2-4. Pearson correlation coefficients between the residual chronology of each site with monthly climate variables: (a) mean temperature and (b) total precipitation. The analysis was conducted over two growing seasons from April of the prior year (lag 1 = t-1) to October of the current year (lag 0 = t). Significant ($p < 0.05$) positive relationships denoted by gray boxes, and significant ($p < 0.05$) negative relationships indicated by black boxes. The number of significant positive and negative correlation coefficients are shown below each figure with the highest number for each underlined. The mean correlation coefficient for each month is also indicated.

(Note: Caption for following figure)

Figure 2-5. Pearson correlation coefficients between the residual chronology of each site with seasonal (3 month periods) climate variables: (a) mean temperature and (b) total precipitation. All possible 3 month periods were considered that spanned two growing seasons from April of the prior year (lag 1 = t-1) to October of the current year (lag 0 = t). The monthly abbreviations indicate the month at which a 3 month period ends. Significant ($p < 0.05$) positive relationships denoted by gray boxes, and significant ($p < 0.05$) negative relationships indicated by black boxes. The number of significant positive and negative correlation coefficients are shown below each figure with the highest number for each underlined. The mean correlation coefficient for each month is also indicated.


a)
Seasonal Period and Lag
J J A S O N D J F M A M J J A S O
1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0
Site
1A 1B 1C 2A 2B 2C 3A 3B 3C 4A 4B 4C 5A 5B 5C 6A 6B
(+r) 5 8 11 6 5 7 5 2 1 1 3 5
(-r) 1 1 6 10 5
(r) .02 -.03 -.20 -.25 -.15 .11 .20 .24 .19 .19 .18 .16 .08 -.00 .06 .12 .17
No. of Significant Correlations and Mean Correlation


b)
Seasonal Period and Lag
J J A S O N D J F M A M J J A S O
1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0
Site
1A 1B 1C 2A 2B 2C 3A 3B 3C 4A 4B 4C 5A 5B 5C 6A 6B
(+r) 2 3 6 8 9 3 1 4 2 2
(-r) 4 2 3 7 3 1 1 1
(r) .04 .05 .18 .25 .25 .00 -.09 -.11 -.10 -.16 -.11 .02 .08 .08 .00 -.04 -.08
No. of Significant Correlations and Mean Correlation

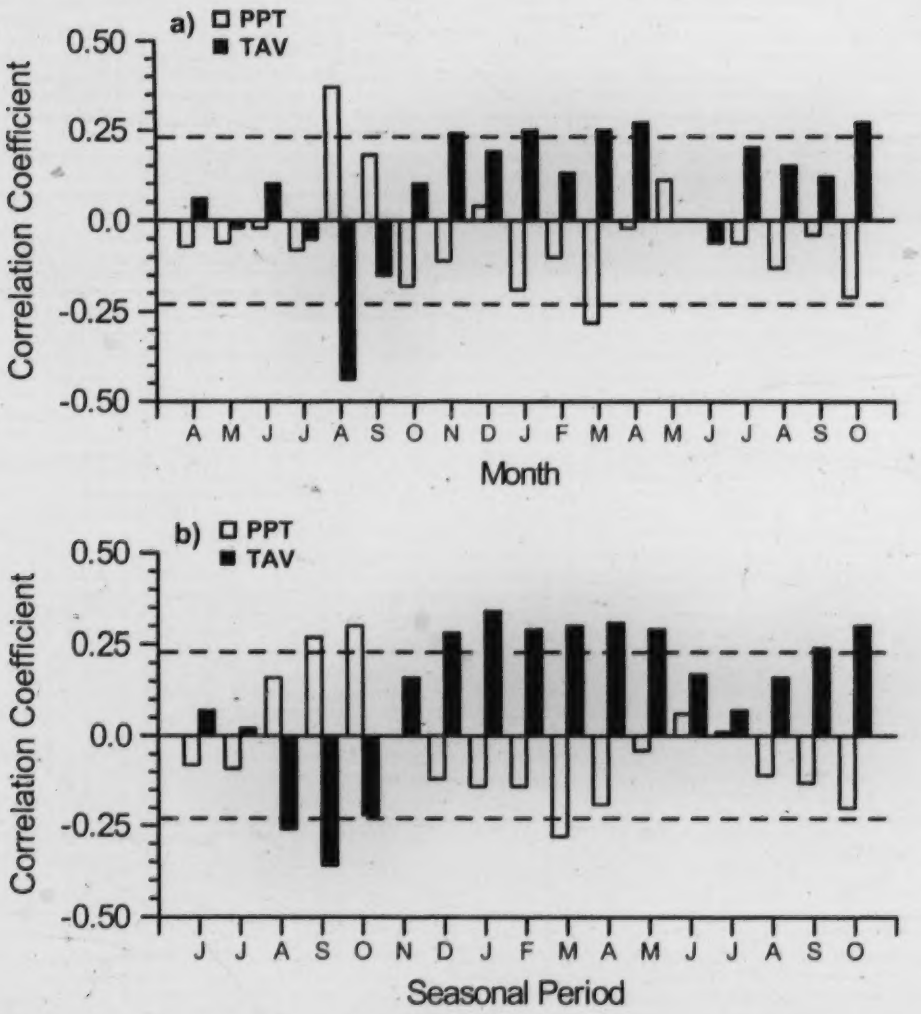


Figure 2-6. Pearson correlation coefficients between the regional residual chronology of all 17 sites combined with regional (a) monthly and (b) seasonal (3 month periods) climate variables: mean temperature (TAV) and total precipitation (PPT). Dashed lines indicate the threshold for significant correlations at $p < 0.05$. Regional climate variables are expressed as anomalies in °C (TAV) or mm (PPT) from the reference period of 1961-1990.

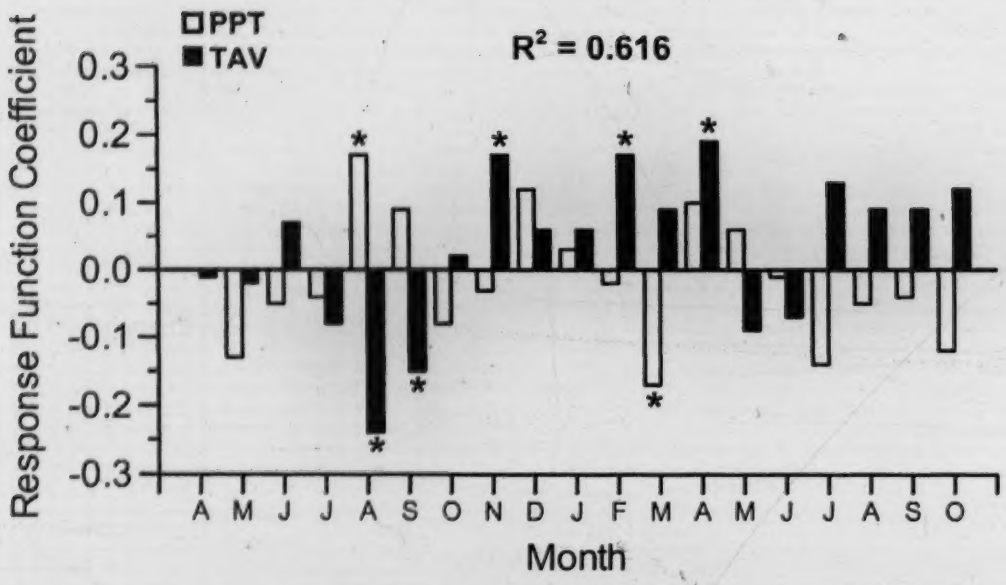


Figure 2-7. Response function coefficients between the regional residual chronology of all 17 sites combined with both regional monthly temperature (TAV) and precipitation (PPT). Significant climate variables are denoted by an asterisk. The R^2 value of the response model indicates the proportion of the variance in radial growth accounted for by the full set of 38 monthly climate variables.

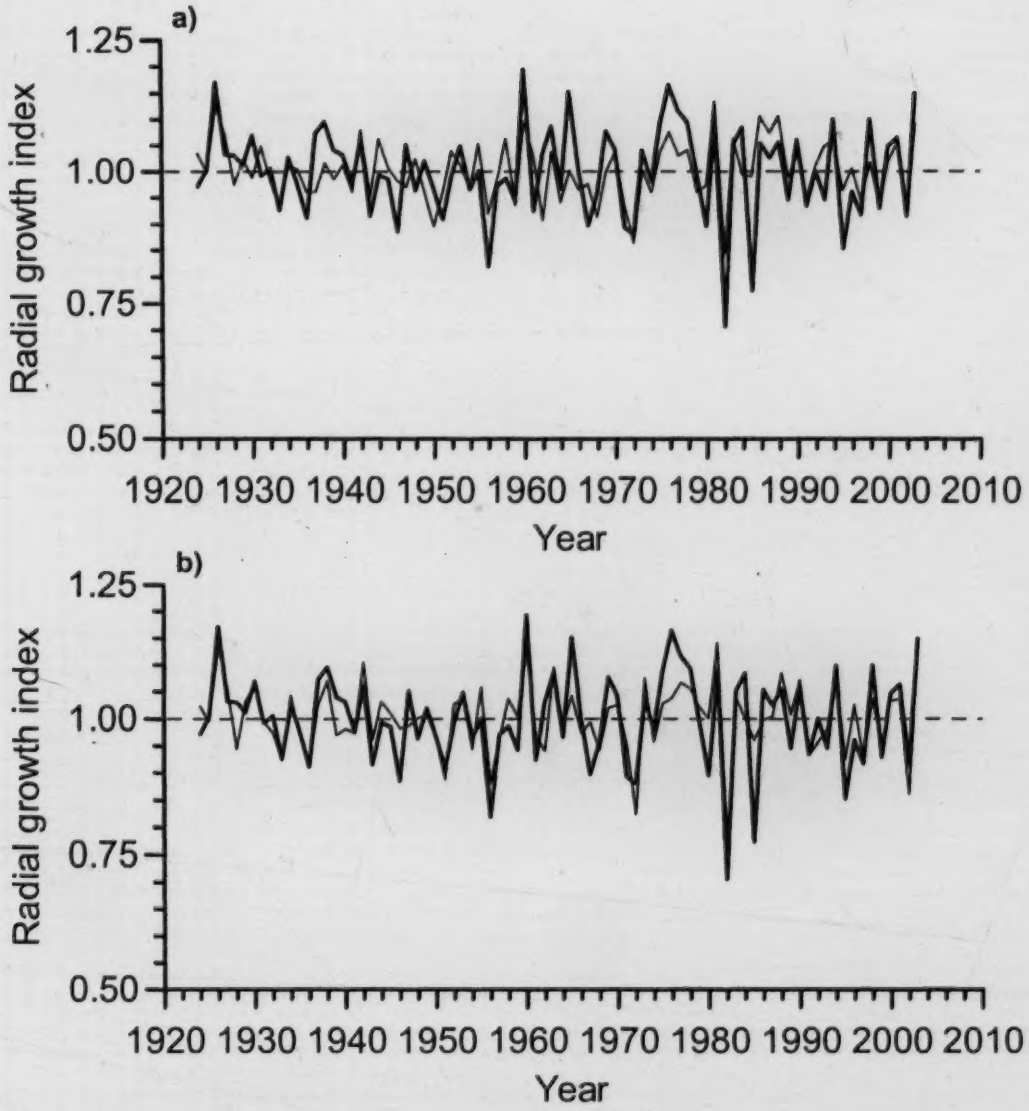


Figure 2-8. The observed (bold line) versus the modeled (thin line) regional radial growth index (RGI) based on (a) the regression model of mean temperature listed in Table 2-3 and (b) response function model of mean temperature and total precipitation in Fig. 2-7.

Chapter III: Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions [2]

Introduction

Trees generally grow in dense stands, and competition for resources induces differentiation of trees into size hierarchies such as diameter size classes (Oliver and Larson 1996). Most tree-ring studies (dendrochronology) involve examining the largest diameter trees to minimize the effect of competition and amplify the climatic signal (Schweingruber et al. 1990; Piutti and Cescatti 1997; Meyer and Bräker 2001). Trees of smaller diameter classes are typically aged in demographic studies (i.e., dendroecology), but there have been few attempts to examine how interannual variations in radial growth – climate relationships may differ between trees of different diameter size classes (Piutti and Cescatti 1997; Cescatti and Piutti 1998; Meyer and Bräker 2001).

The classification of ecological regions in Alberta is based on biophysical factors and is a reflection of how physical environmental factors (i.e., climate) contribute to the development of distinct plant community assemblages (Natural Regions Committee 2006; Samuelson and Rood 2004). Along the eastern slopes of the Rocky Mountains in Alberta, ecoregions are differentiated primarily on the basis of elevational changes in climatic conditions (Natural Regions Committee 2006). Previous studies have examined diameter growth patterns across elevational ecoregions in the Rocky Mountains but did not directly examine growth-climate relationships (Berg et al. 2007).

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[2] A version of this chapter has been accepted for publication in Forest Ecology and Management: In Press.

In contrast, the current study describes the relationships between basal area growth and climate for trees of different diameter size classes and for a broad network of 65 lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) sites spanning a range of elevational ecoregions. The other specific objective was to make projections of basal area growth under different climate change scenarios in the 21st century.

Material and Methods

Site selection and field sampling

The 4 elevational ecoregions (ER) sampled in the cordilleran forests included the Boreal Highlands (HL), Foothills (FH), a grouping of the montane and subalpine zones of the Rocky Mountains (RM), and the montane zone of the Cypress Hills (CH) (Table 3-1; Fig. 3-1). The elevation region with the lowest average elevation was HL, followed by progressively higher average elevations in FH, CH, and RM. Within each region, the elevation generally declined with a corresponding increase in latitude (Natural Regions Committee 2006). HL generally had the lowest mean annual temperatures followed by warmer temperatures in FH, RM and CH (Table 3-1; Fig. 3-1). Total annual precipitation and Climate Moisture Index (CMI) (Hogg 1997) values indicate dry climatic conditions in CH followed by progressively moister climates in HL, FH and RM. Seasonally, summers were warmest and driest in CH, and winters were coldest in HL.

A total of 65 lodgepole pine sites were selected from the Alberta Forest Service permanent sample plot database (Alberta Land and Forest Service 1994). All sites were closed-canopied, even-aged stands of fire origin. The 65 sites covered the predominant latitudinal and elevational range of lodgepole pine in Alberta (Table 3-1; Fig. 3-1).

Stands were selected that had no obvious recent history of disturbances (e.g., fire, insects, or disease). Most of the lodgepole pine stands were sampled from the main geographical range of lodgepole pine in Alberta, except for the 4 sites (901-904) sampled from a disjunct lodgepole pine population located in Cypress Hills Interprovincial Park (Table 3-1; Fig. 3-1).

The first diameter class (DC) was comprised of the three largest diameter trees (hereafter referred to as top diameter trees (T)) selected from a 300 m^2 (radius = 9.77 m) circular plot established at each of the 65 sites within a 50 m buffer zone surrounding each of the provincial government permanent sample plots. At each site, nested within the 300 m^2 plot and sharing the same plot centre, a 200 m^2 (7.98 m radius) circular plot was used to select the other three DCs. The range of tree diameters at breast height (9.1 cm or larger) within the 200 m^2 plot at each site were divided into three DCs (small (S), medium (M), large (L)) such that each DC had equal basal area. A representative tree nearest to the midpoint of each DC was selected at each site. The selected trees of each of the four DCs (S, M, L and T) were taken from the dominant and co-dominant canopy layer in each stand. The selected trees were felled and a cross-sectional disk was sampled at breast height (1.3 m). While there were few instances of trees at the low end of the small diameter size class that did come from the intermediate and suppressed crown classes, the actual trees selected in this study for tree sectioning were from the midpoint of the small diameter class which in turn were exclusively from the dominant/co-dominant canopy layer. A total of 6 trees were sampled at each site except in site 13 in which a suitable S tree could not be found. Consequently, 389 [(65 x 6) – 1] trees were sampled for this study.

Dendrochronological measurements

All sampled disks were sanded with progressively finer grades of sandpaper to highlight annual rings (Stokes and Smiley 1996). All samples were visually crossdated under a binocular microscope to identify any missing and/or false rings (Yamaguchi 1991). For each sample, annual ring width was measured along two radii using an image analysis system (DendroScan: Varem-Sanders and Campbell 1996). Images of disks were scanned at an optical resolution of 1200 d.p.i. Difficult sections of some disks containing extremely narrow rings were measured with a stage micrometer (Velmex: Bloomfield, New York). The visual crossdating and tree-ring measurements were further verified via statistical crossdating with the program COFECHA (Grissino-Mayer 2001). In 12 of the 64 suppressed trees sampled, periods of suppressed growth (ranging from 4-19 years) in the most recent years of growth (ranging from 1985-2003) could not be reliably crossdated and therefore were not measured and excluded from further analysis.

For each tree sample, the mean stem radius at the end of each year of growth was determined by averaging the ring width measurements of the two radii. Basal area increment (cm^2 $year^{-1}$) was calculated using the mean stem radius and the formula for the area of a circle (Hogg et al. 2005). Basal area increments were standardized based on a quadratic, locally weighted regression (Loess) with a neighborhood span equivalent to 20 years using the function *loess* (package *STATS*) in the program R (Arbaugh and Peterson 1993; Venables and Ripley 2002). Basal area index (BAI) was calculated as the ratio of observed basal area increment versus the predicted value from the Loess model. BAI of the three T trees at each site were averaged together. BAI were further summarized by averaging them by ER and DC combinations.

Climate data

Spatially-interpolated climate data for each of the 65 lodgepole pine sites were provided by McKenney et al. (2001) based on the program ANUSPLIN (Hutchinson 2000). The primary climate variables included mean monthly temperature (TAV) and total monthly precipitation (PPT) over the period of 1901-2003. In addition to the monthly scale, 2, 3, 4, 5, 6, and 7 month seasonal periods of the climate variables were also considered. Combined (regionalized) climate data from all sites within each ER and for all sites were used in further analyses. The regionalized climate data were combined by first converting the raw climate data at each site into anomalies in °C (mean temperature) or mm (total precipitation) from their respective mean for the reference period of 1961-1990 (Jones and Hulme 1996). The climate variables of all 65 sites expressed as anomaly values were then averaged together to produce the regional climate variables for each ER or for all ERs combined.

Growth-climate analyses

Relationships between the regional chronologies (all DC combined for each ER or all ERs combined) and regional climate variables were modeled using a step-wise multiple regression analysis, with forward selection, using the function *stepAIC* (package *MASS*) in the program R (Venables and Ripley 2002). The regression model selected for each climate variable set (mean temperature and precipitation) at each scale (monthly and seasonal (2, 3, 4, 5, 6, and 7-month periods)) was selected based on minimizing the value of Akaike's information criterion as long as adding a predictor variable lowered the Akaike's information criterion value by at least 2 (Burnham and Anderson 2002). The

climate variables which were used as the set of possible candidate predictor variables span a 19-month window and covers two growing seasons from April of the prior year (t-1) to October of the current year (t) [apr(t-1)_oct(t)] and over an 80 year period (1924-2003). Seasonal climate variables sharing the same month(s) as those seasonal variables selected earlier in the step-wise sequence were excluded from the regression model. There was limited multicollinearity between the initial pool of monthly predictor variables (e.g., see Appendices III, IV, and V for examples for all 65 sites combined).

The candidate predictor variables for the final regression models consisted of the predictor variables selected for each climate scale. These candidate predictor variables were pooled together from across the climate scales and subjected to a final step-wise regression procedure in order to derive the final regression models. The final regression models for mean temperature and precipitation were each checked separately for multicollinearity between the predictor variables and none was present (all $p \geq 0.05$). However, the regression models of temperature and precipitation could not be combined into a single model because of the issue of multicollinearity between the temperature and precipitation variables. Thus, a monthly climate moisture index (CMI) was calculated as PPT minus potential evapotranspiration, which combines the effect of both precipitation and temperature on moisture regimes (Hogg 1997). Monthly values of potential evapotranspiration were based on a simplified form of the Penman-Monteith equation which involves estimating mean vapour pressure deficit from mean daily minimum and maximum temperature for each month.

Standardized partial regression coefficients were also calculated to help assess the relative importance of the predictor variables in each regression model (Zar 1999). For

each ER and for all ERs combined, the regression models identified for all DC combined was subsequently applied to each of the individual DC. For each predictor climate variable, a 95% confidence interval was constructed for each partial regression coefficient in order to compare them between the DC within each ER or all ERs combined.

Growth projections under future climate change scenarios

The predicted change in climate under two different scenarios and for three periods in the 21st century (2010-2039, 2040-2069, and 2070-2099) relative to the climatic normal period of 1961-1990 were obtained for each of the 65 sites using the program ClimatePP (version 3.0) (Wang et al. 2006). ClimatePP incorporates output from the second generation coupled global climate model (CGCM2) from the Canadian Centre for Climate Modelling and Analysis (CCCma) (Flato and Boer 2001). ClimatePP generates spatially interpolated climate data based on site latitude, longitude, and elevation (Wang et al. 2006). The two climate change scenarios considered here were based on CGCM2 forced with two different IPCC (2001) emission scenarios: A2 and B2. Relative to A2, the B2 emission scenario is characterized by slower human population growth and more emphasis on environmental protection and sustainability; less greenhouse gas emissions are produced resulting in less warming. ClimatePP provides output of climate change scenarios for all calendar months and for all primary climate variables including mean temperature and precipitation. The climate change variables of the 65 sites were averaged together and by elevational region to produce the regional climate change variables.

The regression model of each combination of ER and DC was applied to the regional climate change variables to project growth for the three periods in the 21st century under the two climate change scenarios. The projected BAI was based on the regression models for TAV, PPT and CMI applied separately to the future climate scenarios. The significance of the projected growth estimates were examined in comparison to a 95% confidence interval of the mean expected BAI for the period 1961-1990. The mean estimate of growth was calculated by entering in values of zero for the predictor variables in the regression models of TAV and PPT and therefore is equivalent to the value of the constant of the regression models. The standard error of the mean required to calculate the length of the confidence interval was based on the standard error of the mean of the observed values of BAI for the period 1961-1990 for each ER and DC combination. Projected BAI for the climate scenario periods were also expressed as percentage change relative to the mean BAI for the climatic normal period.

Results

Growth characteristics

The BAI chronologies (based on all DC combined) for each ER and for all ERs combined are presented in Fig. 3-2. The BAI chronology of all ERs combined (Fig. 3-2e) consisted of periods of reduced growth in the late 1950s, early 1970s, early 1980s, and late 1990s, and increased growth in the late 1970s. Within each ER, growth of T trees had strong and significant correlations with the other 3 DCs (all had $r > 0.78$ and $p < 0.0001$), although the strength of the relationship was generally greatest with L trees and slightly decreased with M and S trees (Table 3-2). For all ERs combined, S trees had the

highest percentage of missing rings (0.440 %), compared to M (0.165 %), L (0.099 %), and T (0.068 %) trees.

Growth-climate relationships

The prediction sum of squares (PRESS) were reasonably close to the error sum of squares (SSE) which lends support to the validity of the regression models (Kutner et al. 2004) (Appendix I). Growth was negatively associated with late summer temperature of the prior growing season (t-1) in each ER and for all ERs combined, and included the months of July (t-1), August (t-1), and September (t-1) (Table 3-3). Growth responded positively to mean temperature for the 7-month period of October (t-1) to April of the current growing season (t) for all ERs combined and in HL. Growth in the other ER responded to portions of this 7-month temperature period [T7_oct(t-1)_apr(t)]. In FH and RM, growth responded positively to mean temperature for the 2-month period of October (t-1) to November (t-1), as well as the 3-month period of February (t) and April (t). In CH, growth responded positively to mean temperature for both the 2-month period of November (t-1) to December (t-1), and in February (t). For all DC combined, lodgepole pine responded more to temperature for the period of T7_oct(t-1)_apr(t) versus T3_jul(t-1)_sep(t-1) in HL and for all ERs combined according to the standardized partial regression coefficients. However, the most influential predictor variable was late summer conditions of the prior year in FH [T2_jul(t-1)_aug(t-1)], CH [T2_aug(t-1)_sep(t-1)], and RM [T2_aug(t-1)_sep(t-1)].

Growth was positively associated with summer precipitation in the prior growing season in each ER; for all ERs combined the response was with total precipitation

amounts for the 2-month period of August (t-1) to September (t-1) (Table 3-4). There were differences among ERs in the response to summer precipitation (t-1); growth in HL responded to summer precipitation for the entire summer period, being positively associated with total precipitation amounts for the 5-month period of May (t-1) to September (t-1). In contrast, growth in the other ERs (FH, CH, and RM) responded more to precipitation in late summer (t-1). Growth responded negatively to precipitation amounts for the 6-month period of October (t-1) to March (t) in HL, FH, and for all ERs combined. Growth in RM responded negatively to only a portion of this period, from February (t) to March (t). Growth in HL and CH responded positively to precipitation in early summer of the current year. Growth in HL also responded negatively to late summer precipitation in August (t). The most influential predictor variable for each ER and for all ERs combined was the positive response to summer conditions in the prior growing season. Growth responses to the climate moisture index were very similar to precipitation except for the additional negative influence of moisture conditions in February (t) in CH (Table 3-5).

In each ER, the growth response to climate (temperature, precipitation or moisture index) was always stronger in T versus S trees as measured by the adjusted coefficient of determination (R^2) (Table 3-3; Table 3-4). For all ERs combined, there was a general trend in R^2 across the DCs, with T trees generally having the strongest relationship with climate and a progressively weaker relationship with L, M, and S trees. For each ER and for all ERs combined, and for all predictor variables, the partial regression coefficients had overlapping 95% confidence intervals among the DCs.

Effects of future climate change

The two climate change scenarios had similar rates of warming during the first two projected climate periods (2010-2039, 2040-2069), but the A2 scenario had greater warming than the B2 scenario during 2070-2099 (Table 3-6). In both climate scenarios, the projected rates of winter versus summer warming were similar in each ER except HL, where warming in winter was slightly greater than in summer. Under the A2 scenario, there were projected increases in winter and annual precipitation in each ER, but projected summer precipitation decreased in every ER except FH (Table 3-6). Under the B2 scenario, decreases in summer and annual precipitation are expected in HL, whereas in the other ERs, precipitation is expected to increase (summer, winter and annually). In either scenario, the amount of annual increase in precipitation was generally greatest in RM followed by FH, CH, and HL. However, the moisture index is expected to decline annually and particularly during the summer in each ER, and this indicates that annual increases in precipitation are not sufficient to offset increases in potential evapotranspiration induced by the predicted warming trend.

The projections of percentage increase or decrease in growth relative to the climate normal period (1961-1990) were generally similar among DCs and were on average within 1.1% of each other. Consequently, only the projected estimates for all DCs combined are presented in Fig. 3-3. The projected changes in BAI under all of the precipitation models (regardless of ER, climate scenario, or projected period) did not differ significantly from the 95% confidence interval of mean expected BAI for 1961-1990 (Fig. 3-3). Growth projections based on the moisture index declined significantly in HL for the last two projected periods under either scenario (A2: -4.2%, -6.9%; B2: -4.2%,

-5.7%); growth also declined for the last two periods in CH under the A2 scenario (-4.6%, -8.1%). For either scenario or any of the projected periods, projected BAI in HL based on the temperature regression model, did not differ significantly from 1961-1990. In FH, significant decreases in growth were observed under either climate scenario in the last two projected periods (A2: -3.4%, -5.8%; B2: -3.6%, -5.1%) under the temperature model. Similarly, in CH, significant decreases in growth were observed under the A2 climate scenario for the last two projected periods based on the temperature model (-5.1% and -8.9%). In contrast, significant increases in growth are expected in RM in the last projected period under the A2 climate scenario (5.0%). For all ERs combined, the only significant departures in growth from the climate normal period were under either scenario for the last projected period and based on the temperature model (A2: -3.6%; B2: -2.9%). Under the temperature models and for the last projected period in particular, some of the growth projections were based on temperature conditions outside the range of initial model development.

Discussion

Growth-climate relationships

For all ERs combined, lodgepole pine in Alberta responded to heat and drought stress in late summer of the prior growing season. This lagged climatic response was also found in each ER individually although in HL the response to moisture stress was for the entire summer of the previous year. Lags in response to climatic stress in late summer in pines are likely due to the role of carbohydrate reserves and the multi-year development of buds and foliage (Kozlowski et al. 1991; Owens 2006) and were described in Chapter

II (p. 26) (Chhin et al. 2008). Growth was additionally affected by moisture stress in early summer [May (t) and June (t)] of the year of ring formation in HL and CH, which was expected since these were the driest ER. It is speculated that, based on a strong inverse relationship between precipitation and temperature in August ($r = -0.47$, $p < 0.0001$) in HL, wet Augusts are accompanied by cloudy conditions that decrease surface solar radiation and the resultant cooler temperatures (Dai et al. 1999) lead to an early cessation of radial growth and reduced rates of photosynthesis.

For all ERs combined, growth was also affected by the length of the growing season and degree of winter harshness which was reflected by the negative response to cold conditions and high precipitation spanning the fall of the previous year [October (t-1)] to early spring of the current year [March (t) - April (t)] of ring formation. Possible ecophysiological stresses occurring during winter dormancy (Kozlowski et al. 1991; Havranek and Tranquillini 1995) were described in Chapter II (pp. 27-28) (Chhin et al. 2008). Growth responses to winter conditions varied depending on ER. Growth was inhibited by low temperature (and conversely, milder winters promoted growth) in all winter months at the most northern HL sites which had the coldest winters. The much colder winters in HL compared to the other ER is due to the greater influence of continental polar air masses and the reduced influence of warm, westerly Chinook winds (Natural Regions Committee 2006). The major zone of Chinook winds in Alberta is concentrated primarily in the area of the study sites in RM (Natural Regions Committee 2006). Consequently, it is speculated that the collapse in the direct relationship between growth and winter temperature in the midwinter months in RM is due to the damaging effects of Chinook winds. Chinook winds are characterized as strong, drying winds

which would contribute to crown collisions leading to foliage loss and winter-desiccation injury ('red belt') (Lotan and Critchfield 1990).

Warm springs with low precipitation contribute to earlier snowmelt and soil warming, thus leading to an earlier start to the growing season. All ERs responded to the timing of the start of the growing season except CH, which was expected given that this region generally had the warmest temperatures such that heat accumulation requirements to resume growth were easily met. Monserud et al. (2006a) also identified that site index (height growth over the first 50 years of growth) of lodgepole pine in Alberta showed a strong, positive relationship with spring temperature. They also reported that site index was positively related to summer temperature and uncorrelated with measures of precipitation and winter temperature, all of which are contradicted by this study. This may be because they did not examine interannual variations in growth since the productivity of a stand is represented by a single averaged estimate of site index. Consequently such studies are focused primarily on comparisons with climate normals which precludes the analysis of lagged relationships between growth and climate.

The largest diameter trees are usually sampled in dendrochronological studies in order to minimize the influence of competition on tree growth and partly because they are easier to crossdate. Indeed, in this study, it was more difficult to date the S trees owing to the greater occurrences of missing rings. There was a minor trend in response to climate across the diameter classes since the T trees generally had the strongest relationship with climate with a progressive but only slightly weaker relationship in L, M, and S diameter size classes. For each ER, the mean values of partial regression coefficients were generally similar and had overlapping 95% confidence intervals among the DC. The

general consistency in climatic response may reflect similarities in genetic composition and microclimatic conditions of trees reaching the co-dominant/dominant canopy layer, and possibly even the sharing of carbohydrates among trees of different diameter size classes via root grafts (Fraser et al. 2005). No differences in growth-climate relationships were observed between the largest diameter (dominants) versus the smallest diameter (suppressed) trees of Norway spruce (*Picea abies* (L.) Karst.) and the differences were found to be more related to elevational region (subalpine versus lower montane) (Meyer and Bräker 2001). In contrast, the growth response to high temperature in European beech (*Fagus sylvatica* L.) changed from positive to negative as the competition level increased for trees of progressively smaller diameters (Piutti and Cescatti 1997). Therefore, thinning the lower diameter size classes to maintain the low competition level of large diameter trees may be an effective tool to mitigate the effects of climate change in some species (Cescatti and Piutti 1998; Laurent et al. 2003). However, thinning does not appear to be a viable option for lodgepole pine in Alberta due to the generally uniform response to climate across diameter size classes.

Potential Effects of future climate change

The foothills (FH) represent the main productive region of lodgepole pine in the province of Alberta (Monserud et al. 2006b). Consequently the forecasted declines in productivity in this region late in this century are disturbing. The CH, as would be the case for other 'island forests' surrounded by prairie, are expected to be vulnerable to the effects of climate change because they can lack the ecological resiliency of larger forested areas and also have restricted options for tree migration (Henderson et al. 2002).

Although lodgepole pine forests in CH represents a small proportion of the province wide inventory, the possible future decline of lodgepole pine in CH may result in a decline in the unique biodiversity of this area which includes outlier species or species at the edge of their distribution (Henderson et al. 2002). The projected increase in growth due to climate warming in the RM may not have wide reaching effect since this region represents a small proportion of the productive landbase of lodgepole pine in Alberta.

The decline in productivity of lodgepole pine in FH and CH under climate change could open the door to competitive displacement by other tree species more adapted to the new climate (Loehle 2003). This could mean competitive displacement by trembling aspen (*Populus tremuloides* Michx.) which is present at lower elevations in FH and in CH (Natural Regions Committee 2006). In RM where climate change is expected to lead to increases in growth, lodgepole pine might competitively displace Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and other species near the tree-line.

References

Alberta Land and Forest Service. 1994. Permanent sample plot field procedures manual. Timber Management Branch, Alberta Forest Service, Edmonton, Alberta. Pub. FMOPC 83-03.

Arbaugh, M.J., and Peterson, D.L. 1993. Stemwood production patterns in ponderosa pine: effects of stand dynamics and other factors. Pacific Southwest Research Station, USDA Forest Service, Washington. Research Paper PSW-RP-217.

Berg, K.J., Samuelson, G.M., Willms, C.R., Pearce, D.W., and Rood, S.B. 2007. Consistent growth of black cottonwoods despite temperature variation across elevational ecoregions in the Rocky Mountains. Trees, **21**: 161-169.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Cescatti, A., and Piutti, E. 1998. Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. Forest Ecology and Management, **102**: 213-223.

Chhin, S., Hogg, E.H., Lieffers, V.J., and Huang, S. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany, **86**: 167-178.

Dai, A., Trenberth, K.E., and Karl, T.R. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. Journal of Climate, **12**: 2451-2473.

Flato, G.M., and Boer, G.J. 2001. Warming asymmetry in climate change simulations. Geophysical Research Letters, **28**: 195-198.

Fraser, E.C., Lieffers, V.J., and Landhausser, S.M. 2005. Age, stand density, and tree size as factors in root and basal grafting of lodgepole pine. Canadian Journal of Botany, **83**: 983-988.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, UK.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research, **57**: 205-221.

Havranek, W.M., and Tranquillini, W. 1995. Physiological processes during winter dormancy and their ecological significance. *In* Ecophysiology of coniferous forests. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 95-124.

Henderson, N., Hogg, E.H., Barrow, E., and Dolter, B. 2002. Climate change impacts on the island forests of the Great Plains and the implications for nature conservation policy: the outlook for Sweet Grass Hills (Montana), Cypress Hills (Alberta-Saskatchewan), Moose Mountain (Saskatchewan), Spruce Woods (Manitoba) and Turtle Mountain (Manitoba-North Dakota). Prairie Adaptation and Research Collaborative (PARC), Regina, Sask. Final Rev. Report.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology, **84**: 115-122.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research, **35**: 610-622.

Huang, S., Morgan, D.J., Klappstein, G., Heidt, J., Yang, Y., and Greidanus, G. 2001. Yield tables for seed-origin natural and regenerated lodgepole pine stands.

Alberta Sustainable Resource Development, Edmonton, Alberta. Tech. Rep. Pub. No. T/485.

Hutchinson, M.F. 2000. ANUSPLIN Version 4.1 User Guide. Centre for Resource and Environmental Studies, Australian National University, Canberra ACT 0200, Australia.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson. Cambridge University Press, Cambridge, UK.

Jones, P.D., and Hulme, M. 1996. Calculating regional climatic time series for temperature and precipitation: methods and illustrations. International Journal of Climatology, **16**: 361-377.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.

Kutner, M.H., Nachtsheim, C.J., Neter, J., and Li, W. 2004. Applied linear statistical models. 5th ed. McGraw-Hill, New York, NY.

Laurent, M., Antoine, N., and Joël, G. 2003. Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). Forest Ecology and Management 183, 47-60.

Loehle, C. 2003. Competitive displacement of trees in response to environmental change or introduction of exotics. Environmental Management, **32**: 106-115.

Lotan, J.E., and Critchfield, W.B. 1990. *Pinus contorta* Dougl. Ex. Loud. or Lodgepole pine. *In* Silvics of North America: 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. USDA For. Serv., Washington, DC. Agric. Handbook 654. pp. 302-315

McKenney, D.W., Hutchinson, M.F., Kesteven, J., and Venier, L. 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Canadian Journal of Plant Science, **81**: 129-143

Meyer, F.D., and Bräker, O.U. 2001. Climate response in dominant and suppressed spruce trees, *Picea abies* (L.) Karst., on a subalpine and lower montane site in Switzerland. Écoscience, **8**: 105-114.

Monserud, R.A., Huang, S., and Yang, Y. 2006a. Predicting lodgepole pine site index from climatic parameters in Alberta. Forestry Chronicle, **82**: 562-571.

Monserud, R.A., Huang, S., and Yang, Y. 2006b. Biomass and biomass change in lodgepole pine stands in Alberta. Tree Physiology, **26**: 819-831.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Government of Alberta. Pub. No. T/852.

Oliver, C.C., and Larson, B.C. 1996. Forest stand dynamics. John Wiley and Sons, New York, NY.

Owens, J.N. 2006. Reproductive biology of lodgepole pine. Forest Genetics Council (FGC) of British Columbia. Extension Note 07.

Piutti, E., and Cescatti, A. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Canadian Journal of Forest Research, **27**: 277-284.

Samuelson, G.M., and Rood, S.B. 2004. Differing influences of natural and artificial disturbances on riparian cottonwoods from prairie to mountain ecoregions in Alberta, Canada. Journal of Biogeography, **31**: 435-450.

Schweingruber, F.H., Kairiukstis, L., and Shiyatov, S., 1990. Sample selection. *In* Methods of dendrochronology: Applications in the environmental sciences. *Edited by* E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 95-129.

Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. The University of Arizona Press, Tuscon.

U.S. Geological Survey. 1999. Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. [online]. U.S. Geological Survey, Reston, VA. Available from http://esp.cr.usgs.gov/data/atlas/little/index.html [accessed 2007 January 10].

Varem-Sanders, T.M.L., and Campbell, I.D. 1996. DendroScan: a tree-ring width and density measurement system. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta. Spec. Rep. 10.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York, NY.

Wang T., Hamann, A., Spittlehouse, D.L., and Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology, **26**: 383-397.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research, **21**: 414-416.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, NJ.

Table 3-1. Characteristics of the 65 lodgepole pine study sites and means for elevational ecoregions.

Site	ER[1]	NSR[2]	Elev. (m)	Lat.	Long.	Slope (°)	Aspect	TAV[3] (°C)	PPT[3] (mm)	CMI[3] (cm)	Age[4] (yr)	Absent Rings (%)
2	HL	LB	829	57°24'N	118°33'W	0	–	-1.92	453	7.32	101	0.08
3	HL	LB	766	57°19'N	118°33'W	0	–	-1.52	444	5.02	93	0.36
4	HL	LB	742	57°21'N	119°33'W	0	–	-1.08	444	5.22	95	0
5	HL	LB	773	57°22'N	119°44'W	0	–	-1.14	450	6.50	47	0
6	HL	LB	745	57°18'N	119°57'W	2	W	-0.82	448	5.87	46	0
8	HL	LB	964	57°18'N	118°36'W	0	–	-2.38	473	11.38	131	0
9	HL	UB	1011	56°38'N	119°2'W	3	SW	-1.61	487	12.15	68	0
10	HL	UB	1022	56°39'N	119°2'W	2	N	-1.68	489	12.53	68	0
11	HL	UB	926	56°40'N	119°12'W	2	E	-1.21	476	9.62	66	0
12	HL	UB	925	56°37'N	119°54'W	0	–	-0.78	487	11.26	100	0
13	HL	UB	920	56°40'N	120°0'W	3	SW	-0.74	487	11.37	115	0
14	HL	UB	1027	56°44'N	119°50'W	3	NW	-1.40	500	14.46	66	0
339	HL	LB	770	57°14'N	118°16'W	5	W	-1.50	444	4.95	171	0
16	FH	UF	1317	54°45'N	115°54'W	2	S	-1.18	620	28.20	85	0.10
28	FH	UF	1060	54°24'N	115°35'W	4	SE	0.09	584	18.84	97	0.17
29	FH	UF	1044	54°23'N	115°35'W	3	SE	0.18	581	18.22	102	0.16
38	FH	UF	1023	54°4'N	116°3'W	3	NW	0.82	576	15.10	98	1.22
241	FH	LF	924	54°8'N	116°45'W	0	–	1.88	542	8.51	122	0.20
244	FH	UF	1070	54°6'N	116°59'W	3	S	1.40	559	12.58	103	0.08
246	FH	UF	1140	54°4'N	117°4'W	1	E	1.15	569	14.65	104	0
248	FH	UF	1147	54°4'N	117°8'W	13	W	1.16	568	14.61	99	0
250	FH	LF	1002	54°2'N	117°14'W	10	W	1.91	541	8.62	100	0
251	FH	LF	993	54°3'N	117°14'W	3	NW	1.94	539	8.30	104	0
272	FH	LF	888	54°31'N	117°31'W	0	–	1.97	531	8.09	126	0.40
601	FH	UF	1525	53°29'N	118°12'W	43	S	0.15	631	26.82	84	0.21
105	FH	UF	1433	52°45'N	116°31'W	1	NE	0.74	607	19.83	102	0.33
106	FH	UF	1544	52°44'N	116°30'W	5	E	0.19	633	25.00	108	0.08
107	FH	UF	1640	52°43'N	116°29'W	25	SW	-0.28	656	29.56	107	0.24
110	FH	UF	1673	52°41'N	116°25'W	34	W	-0.42	662	30.76	99	0
131	FH	LF	1121	52°44'N	115°53'W	2	N	2.05	546	7.23	102	0
138	FH	UF	1384	52°36'N	115°57'W	2	NW	0.98	587	16.57	75	0
140	FH	UF	1318	52°31'N	115°57'W	9	SW	1.40	569	12.79	109	0
170	FH	UF	1080	52°59'N	115°59'W	0	–	1.92	549	7.79	99	0
173	FH	UF	1233	53°3'N	115°57'W	0	–	1.12	581	14.76	105	0.16
180	FH	LF	906	53°10'N	115°18'W	2	W	2.24	546	6.16	99	0.17
181	FH	LF	969	53°23'N	115°45'W	0	–	1.73	555	8.62	97	0
425	FH	LF	882	53°30'N	115°33'W	2	NW	1.86	549	7.19	38	0

Table 3-1. Continued.

Site	ER[1]	NSR[2]	Elev. (m)	Lat.	Long.	Slope (°)	Aspect	TAV[3] (°C)	PPT[3] (mm)	CMI[3] (cm)	Age[4] (yr)	Absent Rings (%)
92	FH	LF	1119	52°19'N	115°14'W	0	E	2.41	559	7.67	105	0
95	FH	LF	1244	52°22'N	115°21'W	11	N	1.78	579	12.45	104	0.24
152	FH	UF	1532	52°9'N	115°27'W	38	W	0.58	614	21.16	93	0
154	FH	UF	1718	52°4'N	115°29'W	2	N	-0.31	648	28.64	97	0
160	FH	UF	1372	52°22'N	115°38'W	12	SE	1.21	586	15.47	73	0
161	FH	UF	1347	52°21'N	115°38'W	3	SE	1.34	580	14.27	74	0
162	FH	UF	1519	52°20'N	115°42'W	25	SE	0.52	611	21.14	75	0
166	FH	LF	1351	51°56'N	115°11'W	3	E	1.70	573	11.98	74	0.11
510	FH	UF	1471	51°22'N	115°0'W	0	–	1.76	561	11.29	81	0.11
540	FH	UF	1604	51°27'N	115°3'W	16	NW	1.01	590	17.29	102	0.08
542	FH	UF	1611	51°30'N	115°5'W	15	S	0.91	593	17.98	100	0.25
567	FH	LF	1218	51°59'N	114°52'W	0	–	2.19	546	7.49	41	0
428	RM	SA	1735	49°45'N	114°29'W	15	S	1.27	745	34.30	86	0.10
461	RM	SA	1663	50°2'N	114°33'W	4	SW	1.38	690	27.08	80	0
508	RM	MN	1602	49°21'N	114°8'W	5	N	2.44	766	30.97	101	0.17
509	RM	MN	1460	49°18'N	114°17'W	11	W	3.07	734	24.60	85	0
512	RM	MN	1549	49°21'N	114°9'W	15	N	2.71	748	27.98	102	0.25
513	RM	SA	1722	49°49'N	114°29'W	15	E	1.29	731	32.57	79	0
516	RM	SA	1649	50°3'N	114°26'W	4	E	1.47	674	24.87	81	0.21
517	RM	SA	1702	50°4'N	114°26'W	8	SE	1.18	689	27.72	83	0
518	RM	MN	1668	49°40'N	114°29'W	12	E	1.68	735	31.64	80	0
531	RM	SA	1585	50°24'N	114°42'W	2	S	1.49	639	19.96	83	0
532	RM	SA	1730	50°16'N	114°35'W	16	W	0.85	691	28.87	132	0
537	RM	SA	1773	50°15'N	114°35'W	10	W	0.65	706	31.43	130	0.13
901	CH	MN	1314	49°41'N	110°11'W	2	NE	2.28	411	-11.84	132	0.64
902	CH	MN	1299	49°41'N	110°10'W	8	NE	2.34	407	-12.55	131	2.04
903	CH	MN	1465	49°37'N	110°20'W	6	SW	1.77	438	-5.96	112	0
904	CH	MN	1450	49°37'N	110°20'W	10	SW	1.84	434	-6.68	113	0.07

Elevational regions (means)

			TAV (°C)			PPT (mm)			CMI (cm)		
ER	Elev.	Age	Sum.[5]	Win.[5]	Ann.[5]	Sum.	Win.	Ann.	Sum.	Win.	Ann.
HL	878	90	11.56	-15.68	-1.37	247	110	468	-5.16	10.99	9.05
FH	1262	94	11.01	-9.62	1.11	324	111	581	0.95	10.74	15.43
RM	1653	94	10.27	-7.36	1.62	276	218	712	-3.79	21.31	28.50

[1] ER, elevational region abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains.

[2] NSR, natural subregion abbreviations: LB, Lower Boreal Highlands; UB, Upper Boreal Highlands; LF, Lower Foothills; UF, Upper Foothills; MN, Montane; SA, Subalpine

[3] Climate variable abbreviations: TAV, mean annual temperature; PPT, total annual precipitation; CMI, climate moisture index based on PPT minus potential evapotranspiration (Hogg 1997). Climate variables determined for annual period of January-December from 1961-1990.

[4] Age at breast height

[5] Summer (sum.) is defined as the 4-month period of May-August; winter (win.) is defined as 4-month period of November-February; and annual (ann.) is the 12-month period of January-December.

Table 3-2. Chronology intercorrelations between the top diameter class and other diameter classes (S, M, and L) by elevational ecoregion and overall.

ER	S	M	L
HL	0.864	0.894	0.916
FH	0.886	0.921	0.935
CH	0.786	0.855	0.887
RM	0.814	0.782	0.859
ALL	0.922	0.941	0.961

Note: All correlation coefficients are statistically significant at $p < 0.0001$. ER abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ALL, all ERs combined. DC abbreviations: S, small; M, medium; L, large.

Table 3-3. Regression models relating basal area index (BAI) with temperature (T) variables across elevational regions (ERs) and diameter classes (DCs) and for all 65 sites combined.

ERs/DCs	Regression model				Adj. R^2
HL	C	T3_jul(t-1)_sep(t-1)	T7_oct(t-1)_apr(t)		
S	0.992	–0.02454 (-0.215)	0.01833 (0.372)		0.154
M	0.993	–0.03703 (-0.314)	0.02105 (0.412)		0.235
L	0.991	–0.02415 (-0.192)	0.02398 (0.440)		0.201
T	0.987	–0.01973 (-0.180)	0.02479 (0.522)		0.276
All	0.990	–0.02646 (-0.238)	0.02221 (0.461)		0.238
FH	C	T2_jul(t-1)_aug(t-1)	T2_oct(t-1)_nov(t-1)	T3_feb(t)_apr(t)	
S	0.998	–0.03790 (-0.404)	0.01557 (0.404)	0.00708 (0.181)	0.330
M	0.998	–0.03988 (-0.454)	0.01353 (0.374)	0.00698 (0.190)	0.350
L	0.999	–0.03514 (-0.430)	0.01036 (0.308)	0.00814 (0.238)	0.294
T	0.998	–0.03632 (-0.451)	0.01265 (0.382)	0.00782 (0.232)	0.367
All	0.998	–0.03732 (-0.451)	0.01300 (0.381)	0.00751 (0.217)	0.361
CH	C	T2_aug(t-1)_sep(t-1)	T2_nov(t-1)_dec(t-1)	T1_feb(t)	
S	0.980	–0.04664 (-0.375)	0.00945 (0.157)	0.01044 (0.284)	0.149**
M	0.995	–0.03676 (-0.459)	0.00806 (0.208)	0.00716 (0.302)	0.226
L	0.989	–0.05106 (-0.456)	0.00975 (0.180)	0.00951 (0.287)	0.208
T	0.991	–0.04616 (-0.477)	0.01029 (0.220)	0.01016 (0.355)	0.270
All	0.989	–0.04549 (-0.480)	0.00950 (0.207)	0.00924 (0.329)	0.254
RM	C	T2_aug(t-1)_sep(t-1)	T2_oct(t-1)_nov(t-1)	T3_feb(t)_apr(t)	
S	1.000	–0.02320 (-0.320)	0.01033 (0.200)	0.01606 (0.332)	0.163
M	0.998	–0.03207 (-0.465)	0.01338 (0.272)	0.01715 (0.372)	0.298
L	0.999	–0.03034 (-0.446)	0.00967 (0.199)	0.01797 (0.395)	0.281
T	0.998	–0.02259 (-0.362)	0.00811 (0.183)	0.01776 (0.426)	0.248
All	0.999	–0.02702 (-0.429)	0.01042 (0.232)	0.01713 (0.407)	0.285
All	C	T3_jul(t-1)_sep(t-1)	T7_oct(t-1)_apr(t)		
S	0.998	–0.03397 (-0.403)	0.01841 (0.444)		0.281
M	0.999	–0.03502 (-0.430)	0.01780 (0.443)		0.299
L	0.999	–0.03476 (-0.428)	0.01982 (0.496)		0.340
T	0.997	–0.03141 (-0.414)	0.01989 (0.533)		0.365
All	0.998	–0.03378 (-0.429)	0.01900 (0.489)		0.335

Note: For Tables 3-3, 3-4 and 3-5, the first term in the regression model is the constant (C). The predictor variables are labelled accordingly: The first letter identifies the climate variable (T, temperature; P, precipitation; M, moisture index) and the number immediately following indicates the scale of the climate variable. For seasonal climate variables (scales 2-7), the term following the first underscore is the month and lag of the start of the seasonal period, while the last term is the month and lag of the end of the seasonal period. Next to the partial regression coefficient of each predictor variable is the corresponding standardized (β) coefficient (Zar 1999) enclosed in parentheses. All regression models are statistically significant at $p < 0.001$ unless otherwise indicated (*, p

< 0.05; **, p < 0.01). ER abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ALL, all ERs combined. DC abbreviations: S, small; M, medium; Large, large; T, top; ALL, all DC combined.

Table 3-4. Regression models relating basal area index (BAI) with precipitation (P) variables across elevational regions (ERs) and diameter classes (DCs) and for all 65 sites combined.

ERs/ DCs	Regression model					Adj. R^2
HL	C	P5_may(t-1)_sep(t-1)	P6_oct(t-1)_mar(t)	P1_may(t)	P1_aug(t)	
S	0.997	0.000504 (0.341)	–0.000520 (-0.206)	0.001200 (0.267)	–0.000766 (-0.202)	0.271
M	0.996	0.000560 (0.365)	–0.000611 (-0.234)	0.001137 (0.245)	–0.000962 (-0.245)	0.317
L	0.996	0.000591 (0.361)	–0.000561 (-0.201)	0.001635 (0.330)	–0.001293 (-0.308)	0.385
T	0.990	0.000484 (0.340)	–0.000688 (-0.283)	0.000851 (0.197)	–0.001028 (-0.281)	0.325
All	0.995	0.000534 (0.369)	–0.000598 (-0.242)	0.001207 (0.275)	–0.001018 (-0.274)	0.361
FH	C	P1_aug(t-1)	P6_oct(t-1)_mar(t)			
S	1.002	0.000899 (0.331)	–0.000485 (-0.253)			0.193
M	1.003	0.000994 (0.390)	–0.000559 (-0.311)			0.288
L	1.003	0.000839 (0.354)	–0.000524 (-0.313)			0.257
T	1.002	0.000931 (0.399)	–0.000559 (-0.339)			0.321
All	1.002	0.000917 (0.382)	–0.000532 (-0.313)			0.283
CH	C	P2_aug(t-1)_sep(t-1)	P1_jun(t)			
S	0.976	0.001044 (0.231)	0.000999 (0.199)			0.058*
M	0.995	0.001018 (0.350)	0.000575 (0.178)			0.116**
L	0.983	0.001363 (0.335)	0.001441 (0.319)			0.166
T	0.985	0.001050 (0.299)	0.001311 (0.336)			0.156
All	0.985	0.001129 (0.328)	0.001090 (0.285)			0.144
RM	C	P2_aug(t-1)_sep(t-1)	P2_feb(t)_mar(t)			
S	0.995	0.000698 (0.397)	–0.000651 (-0.213)			0.190
M	0.994	0.000598 (0.357)	–0.000590 (-0.203)			0.153
L	0.996	0.000763 (0.461)	–0.000612 (-0.213)			0.247
T	0.994	0.000708 (0.467)	–0.000597 (-0.227)			0.260
All	0.995	0.000693 (0.453)	–0.000603 (-0.227)			0.246
All	C	P2_aug(t-1)_sep(t-1)	P6_oct(t-1)_mar(t)			
S	0.999	0.000598 (0.293)	–0.000435 (-0.240)			0.153
M	1.000	0.000656 (0.332)	–0.000469 (-0.268)			0.201
L	1.000	0.000646 (0.329)	–0.000547 (-0.313)			0.232
T	0.998	0.000621 (0.338)	–0.000522 (-0.320)			0.246
All	0.999	0.000630 (0.330)	–0.000495 (-0.292)			0.217

Note: See footnotes in Table 3-3. Precipitation variables are in units of total mm for the indicated monthly or seasonal period.

Table 3-5. Regression models relating basal area index (BAI) with moisture index (M) variables across elevational regions (ERs) and diameter classes (DCs) and for all 65 sites combined.

ERs/ DCs	Regression model					Adj. R^2
HL	C	M5_may(t-1)_sep(t-1)	M6_oct(t-1)_mar(t)	M1_may(t)	M1_aug(t)	
S	1.000	0.00421 (0.387)	-0.00483 (-0.209)	0.01007 (0.305)	-0.00608 (-0.223)	0.295
M	1.000	0.00471 (0.418)	-0.00618 (-0.258)	0.00953 (0.279)	-0.00749 (-0.265)	0.356
L	0.998	0.00483 (0.402)	-0.00599 (-0.234)	0.01334 (0.366)	-0.01066 (-0.354)	0.431
T	0.992	0.00381 (0.364)	-0.00699 (-0.314)	0.00729 (0.229)	-0.00868 (-0.330)	0.365
All	0.997	0.00439 (0.413)	-0.00603 (-0.267)	0.01009 (0.313)	-0.00828 (-0.311)	0.402
FH	C	M1_aug(t-1)	M6_oct(t-1)_mar(t)			
S	1.004	0.00677 (0.352)	-0.00458 (-0.276)			0.227
M	1.005	0.00753 (0.417)	-0.00505 (-0.324)			0.327
L	1.004	0.00637 (0.379)	-0.00475 (-0.328)			0.293
T	1.004	0.00713 (0.430)	-0.00523 (-0.367)			0.380
All	1.004	0.00695 (0.408)	-0.00490 (-0.334)			0.327
CH	C	M2_aug(t-1)_sep(t-1)	M1_feb(t)	M1_jun(t)		
S	0.976	0.00841 (0.307)	-0.03120 (-0.209)	0.00778 (0.191)		0.117**
M	0.995	0.00742 (0.420)	-0.01910 (-0.198)	0.00525 (0.200)		0.192
L	0.984	0.01005 (0.406)	-0.02886 (-0.214)	0.01093 (0.298)		0.232
T	0.985	0.00833 (0.390)	-0.03316 (-0.285)	0.01011 (0.319)		0.265
All	0.985	0.00861 (0.412)	-0.02786 (-0.244)	0.00857 (0.276)		0.236
RM	C	M2_aug(t-1)_sep(t-1)	M2_feb(t)_mar(t)			
S	0.997	0.00457 (0.379)	-0.00704 (-0.244)			0.187
M	0.996	0.00446 (0.388)	-0.00634 (-0.231)			0.188
L	0.997	0.00514 (0.453)	-0.00665 (-0.246)			0.252
T	0.995	0.00455 (0.437)	-0.00665 (-0.268)			0.249
All	0.996	0.00468 (0.446)	-0.00659 (-0.263)			0.255
All	C	M2_aug(t-1)_sep(t-1)	M6_oct(t-1)_mar(t)			
S	1.000	0.00407 (0.314)	-0.00443 (-0.280)			0.186
M	1.001	0.00440 (0.352)	-0.00478 (-0.312)			0.238
L	1.001	0.00440 (0.353)	-0.00546 (-0.358)			0.276
T	0.999	0.00409 (0.351)	-0.00537 (-0.377)			0.291
All	1.000	0.00424 (0.350)	-0.00502 (-0.339)			0.258

Note: See footnotes in Table 3-3. Moisture index variables are in units of total cm for the indicated monthly or seasonal period.

Table 3-6. Change in climate characteristics across elevation regions (ERs) for 3 periods in the 21st century (2010-2039, 2040-2069, and 2070-2099) under two climate change scenarios (CCS: A2 and B2).

	2010-2039			2040-2069			2070-2099		
CCS/Climate/ER	Sum.	Win.	Ann.	Sum.	Win.	Ann.	Sum.	Win.	Ann.
A2									
TAV (°C)									
HL	1.2	1.4	1.2	2.4	2.9	2.5	4.2	4.9	4.2
FH	1.2	1.2	1.1	2.4	2.4	2.4	4.2	4.1	4.1
CH	1.4	1.5	1.6	3.0	3.1	3.3	5.1	5.3	5.7
RM	1.2	1.2	1.3	2.6	2.5	2.7	4.4	4.3	4.7
ALL	1.2	1.2	1.2	2.5	2.6	2.5	4.3	4.4	4.3
PPT (mm)									
HL	-3.5	2.4	2.3	-8.5	5.2	3.8	-14.3	8.5	6.0
FH	5.4	4.0	15.2	11.5	7.5	31.4	19.7	13.1	54.3
CH	-1.8	1.5	4.3	-3.5	2.5	7.5	-5.0	4.5	12.5
RM	-0.3	7.8	17.4	-2.3	16.8	35.6	-4.1	29.0	61.8
ALL	2.1	4.2	12.4	4.0	8.5	25.2	7.0	14.6	43.4
CMI (cm)									
HL	-2.8	0.2	-3.1	-5.8	0.5	-6.6	-9.9	0.8	-11.0
FH	-2.3	0.4	-3.1	-4.7	0.5	-6.1	-8.1	0.7	-10.3
CH	-4.6	0.0	-7.5	-9.3	-0.3	-16.1	-16.5	-0.7	-28.6
RM	-2.7	0.7	-3.5	-6.2	1.3	-8.1	-10.9	2.2	-14.6
ALL	-2.6	0.4	-3.4	-5.5	0.6	-7.2	-9.5	0.9	-12.4
B2									
TAV (°C)									
HL	1.3	1.6	1.3	2.2	2.7	2.3	3.1	3.8	3.1
FH	1.3	1.2	1.2	2.2	2.0	2.1	3.1	2.9	2.9
CH	1.6	1.6	1.7	2.7	2.7	2.9	3.8	3.8	4.0
RM	1.4	1.2	1.3	2.4	2.1	2.3	3.3	2.9	3.2
ALL	1.4	1.3	1.3	2.3	2.2	2.2	3.2	3.1	3.0
PPT (mm)									
HL	-7.2	2.8	-2.3	-11.6	4.7	-3.5	-16.7	6.6	-5.0
FH	6.0	4.0	13.8	10.0	6.6	23.1	13.7	9.3	32.1
CH	0.8	1.0	6.5	0.6	2.4	11.3	1.8	3.7	16.6
RM	4.1	7.3	21.9	6.9	12.3	36.3	9.4	17.3	50.6
ALL	2.7	4.2	11.6	4.5	7.0	19.5	6.1	9.9	27.1
CMI (cm)									
HL	-3.6	0.3	-4.1	-5.9	0.5	-7.0	-8.2	0.7	-9.6
FH	-2.6	0.4	-3.4	-4.4	0.5	-5.8	-6.1	0.6	-7.9
CH	-4.5	0.0	-7.2	-7.6	-0.2	-12.3	-10.6	-0.3	-17.4
RM	-2.7	0.7	-3.1	-4.8	1.0	-5.7	-6.8	1.4	-8.0
ALL	-2.9	0.4	-3.8	-5.0	0.6	-6.4	-6.9	0.7	-8.8

Note: Climate variables are expressed as anomalies relative to the normal reference period of 1961-1990. ER abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ALL, all ERs combined. Summer (sum.) is defined as the 4-month period of May-August; winter (win.) is defined as 4-month period of November-February; and annual (ann.) is the 12-month period of January-December. Temperature (TAV) changes is in °C; precipitation (PPT) in units of total mm; and climate moisture index (CMI) in units of total cm for the 4-month or 12-month periods.

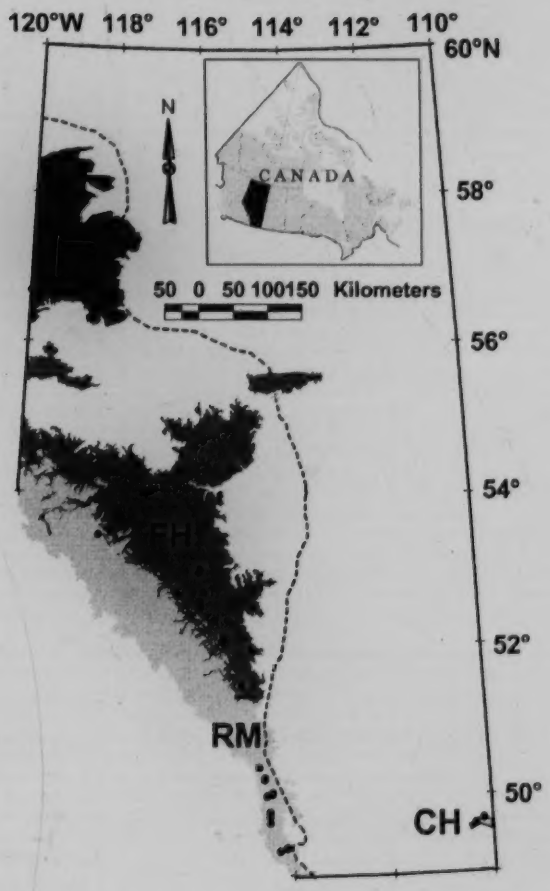

Figure 3-1. Distribution of the 65 lodgepole pine sites in the cordilleran forests of Alberta. West of the dashed line is the main geographic range of lodgepole pine in Alberta (U.S. Geological Survey, 1999). Elevational ecoregion (ER) abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains.

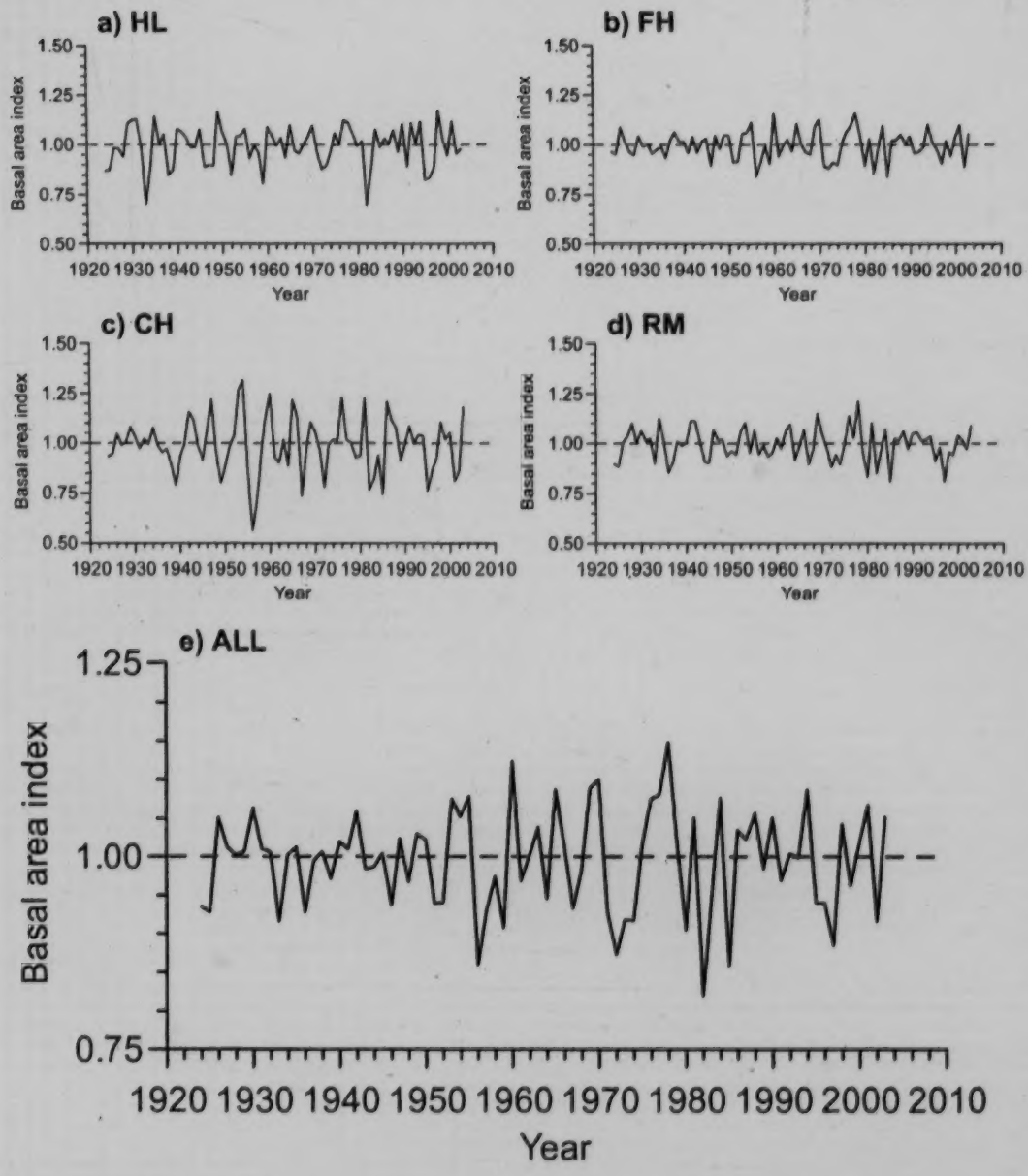

Figure 3-2. Basal area index (BAI) of all diameter classes (small, medium, large, top) combined for each of four elevation regions (HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains) (a-d) and for all 65 lodgepole pine sites (e).

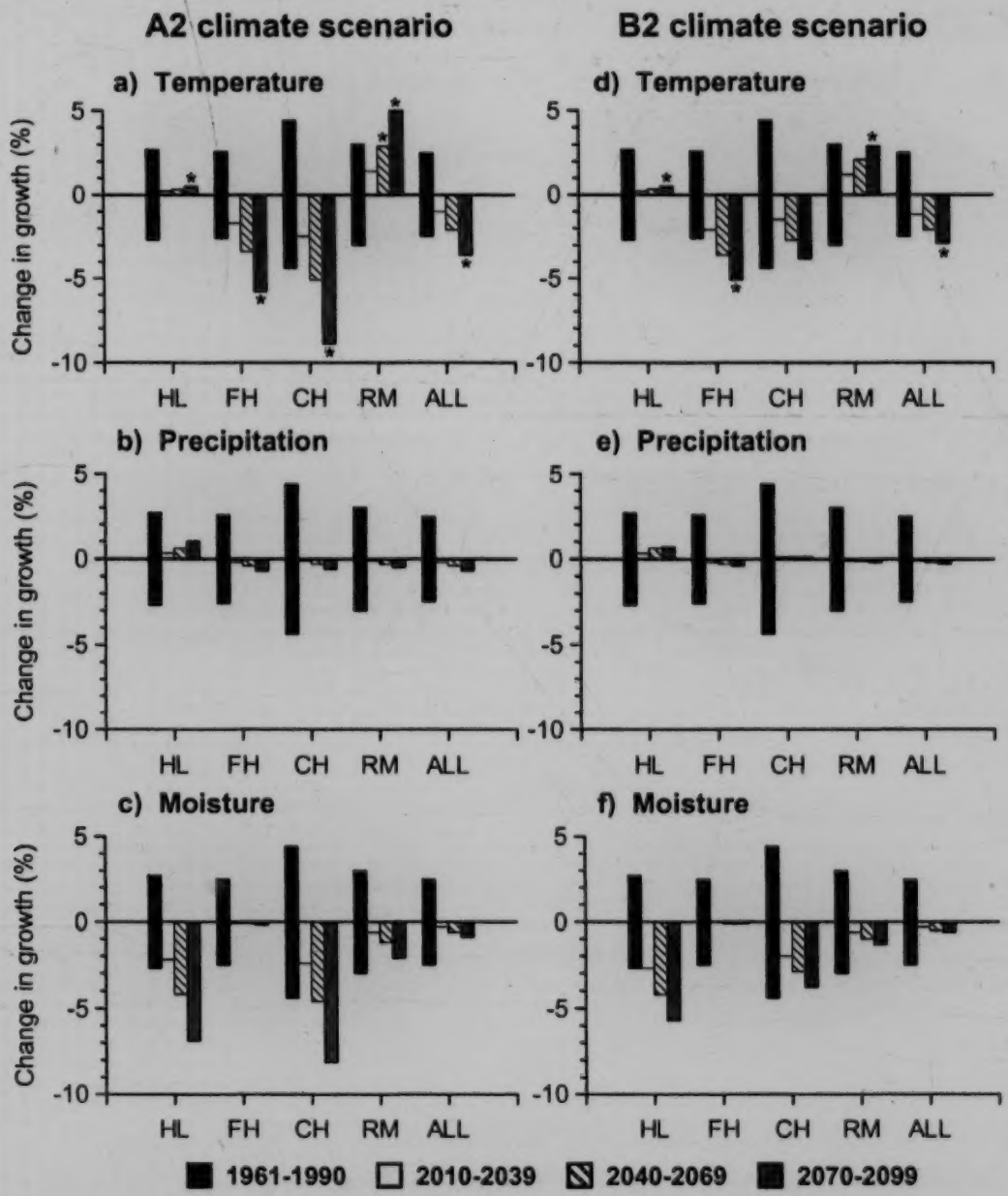

Figure 3-3. Projected percent change of growth variables across elevational ecoregions for 3 future periods in the 21st century under two climate change scenarios (A2 and B2). The projected estimates are based on applying separately the regression models for temperature (TAV, Table 3-3), precipitation (PPT, Table 3-4), and moisture index (CMI, Table 3-5) to the future climate scenarios. The lower and upper limits of a 95% confidence interval of the mean for the control period (1961-1990) and growth projections for the climate scenario periods are expressed as percentage change relative to the mean growth for the control period. Elevational region (ER) abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ; ALL, all ERs combined. Asterisks indicate that growth is projected for a period in which at least one of the climate variables is outside the range of initial model development.

Chapter IV: Growth of the upper stem of lodgepole pine is affected by climate differently than the lower stem

Introduction

In dendrochronological studies, trees are usually sampled from the vicinity of the stem base, particularly at the standard breast height (1.3 m), where increment core samples are traditionally extracted from (Schweingruber et al. 1990; Chhin and Wang 2005). An underlying assumption of most radial growth-climate studies is that radial growth at breast height and its response to climate is implicitly considered a representative proxy for whole stem growth patterns and climatic response, but these assumptions have not usually been validated. Stem analysis of trees can be used to assess whole stem growth patterns, particularly by determining interannual volume increment. The paucity of detailed stem analysis studies is partly because such studies require destructive sampling, and that subsequent sample processing (i.e., sanding) and detailed annual tree ring measurement is extremely resource intensive (LeBlanc 1990). Nonetheless, there have been a number of stem analysis studies which have been conducted in relation to tree growth and development (Duff and Nolan 1953; Duff and Nolan 1957; Fayle and MacDonald 1977; Clyde and Titus 1987), tree allometric relationships (LeBlanc 1990), stand dynamics (Arbaugh and Peterson 1993), insect defoliation (Hennigar et al. 2007), wind (Meng et al. 2006), and silvicultural treatments (Tasissa and Burkhart 1997; Makinen et al. 2002). In contrast, relatively fewer attempts have been made to relate growth patterns at different positions and portions of the bole to climatic variables (e.g., Corona et al. 1995; Bouriaud et al. 2005).

It is generally understood that growth responses to climate in lodgepole pine and other northern conifers derived from the lower sections in the bole (e.g., standard breast height) is driven mainly by climatic conditions and their effect on food reserves accumulated in the seasons (e.g., summer, fall, winter, spring) leading up to the growing season year of ring formation (Fritts 1976; Kozlowski et al. 1993; Chhin et al. 2008). Little is understood, however, of the growth responses to climate of other portions of the stem but it has been postulated that growth higher up the stem is more affected by climate and photosynthate produced in the current growing season in the year of ring formation (Fritts 1976).

In this study, a total of 389 trees were sampled across a network of 65 lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) sites in Alberta using detailed stem analysis in order to examine interannual patterns of basal area increment and volume increment at different positions and portions of the stem in relation to climate. Specific objectives were to examine whether the climatic response of interannual growth in basal area at breast height is similar to interannual variation in volume increment of the whole stem or the upper portion of the stem derived from detailed stem analysis. Projections of growth of the different portions of the stem were also examined under different climate change scenarios in the 21st century.

Materials and Methods

Site selection and field sampling

The 4 elevational ecoregions (ER) sampled in the cordilleran forests of Alberta included the Boreal Highlands (HL), Foothills (FH), Rocky Mountains (RM), and the

Cypress Hills (CH) (Natural Regions Committee 2006) (Table 3-1; Fig. 3-1). A total of 65 lodgepole pine sites were selected from the permanent sample plot network of the Alberta Forest Service (Alberta Land and Forest Service 1994) (Table 3-1; Fig. 3-1), and trees at each site were selected from four diameter classes as described in Chapter III (p. 52). The selected trees were felled and cross-sectional (XS) disks were sampled at 11 positions along the stem of each tree which first included: XS-1, 0.3 m (stump height (SH)); and XS-2, 1.3 m (breast height (BH)) (Fig. 4-1). The remaining 9 disks (XS-3 to XS-11) were obtained along equally spaced points from different relative proportions of the tree stem between breast height to the top of the tree (i.e., tree height above breast height (AB) = total tree height – 1.3 m). A total of 6 trees were sampled at each site except for one site in HL in which a suitable small diameter tree could not be found. Consequently, a grand total of 389 trees and 4279 disk sections were sampled for this study (Table 4-1).

Dendrochronological measurements

All sampled disks were sanded with progressively finer grits of sandpaper to highlight annual rings (Stokes and Smiley 1996), and were visually crossdated under a binocular microscope to identify any missing and/or false rings (Yamaguchi 1991). For each sample, annual ring width was measured along two radii using image analysis systems and disk images were scanned in at an optical resolution of 1200 d.p.i. (DendroScan: Varem-Sanders and Campbell 1996; CDendro and CooRecorder: Saltsjobaden, Sweden). Difficult sections of some disks containing extremely narrow rings were measured with a stage micrometer (Velmex: Bloomfield, New York). The

visual crossdating and tree-ring measurements were further verified with the program COFECHA (Grissino-Mayer 2001). In 14 of the 64 suppressed trees sampled, periods of suppressed growth (mean of 9 years) in the later stage of growth (mean range of 1995-2003) could not be reliably crossdated and therefore were not measured and excluded from further analysis.

For each disk section, basal area (BA) increment ($cm^2 \cdot year^{-1}$) was calculated based on the average ring width measurements of the two radii (Hogg et al. 2005). The ratio of BH_{BA} (basal area growth at breast height) to US_{BA} (average of basal area growth of XS-7, XS-8, XS-9, XS-10 and XS-11) was determined for each tree and is denoted as BH_R. Annual volume (V) increment was determined for the portion of the stem from the breast height level to the top of the tree (AB_V: all XS except XS-1) and for the upper stem portion (US_V: includes XS-7, XS-8, XS-9, XS-10 and XS-11) (Fig. 4-1). Volume was determined using the function *StemAnalysis* (package *treeglia*) in the program R (Venables and Ripley 2002; Bascietto and Searascia-Mugnozza 2004).

Each interannual basal area, volume increment, and breast height ratio series were standardized based on a quadratic, locally weighted regression (Loess) with a neighborhood span equivalent to 20 years using the function *loess* (package *STATS*) in the program R (Arbaugh and Peterson 1993; Venables and Ripley 2002). Basal area index (BAI), volume index (VI), and breast height ratio index (RI) chronologies were calculated as the ratio of their respective observed versus predicted values from the Loess model. BAI, VI, and RI chronologies of the three top diameter trees at each site were averaged together. BAI, VI, and RI chronologies from all diameter classes (small, medium, large, and top) were further summarized by averaging them for each ER. The

first 5 years of each chronology was not included in this regional averaging process in order to limit the influence of the juvenile growth phase of lodgepole pine. Relationships between BAI growth at breast height (BH_{BAI}) and other growth variables (SH_{BAI}, AB_{VI}, US_{VI}, BH_{RI}) were examined using Pearson correlation analysis. The degree of interannual growth variability in each regional chronology was assessed by calculating mean sensitivity (Douglass 1920; Fritts 1976).

Growth-climate analyses

Climate data (mean monthly temperature (TAV), total monthly precipitation (PPT), and climate moisture index (CMI: Hogg 1997)) was obtained for each of the 65 lodgepole pine sites (Hutchinson 2000; McKenney et al. 2001) and combined (regionalized) (Jones and Hulme 1996) in the same manner as described in Chapter III (p. 54). Relationships between the regional chronologies (BH_{BAI}, SH_{BAI}, AB_{VI}, US_{VI}, BH_{RI}) and regional climate variables (TAV, CMI) were modeled using a step-wise multiple regression analysis, with forward selection, using the function *stepAIC* (package *MASS*) in the program R (Burnham and Anderson 2002; Venables and Ripley 2002). This regression analysis was conducted in the same manner as described in Chapter III (pp. 54-55) except that the analysis was conducted over a 51 year period (1953-2003). Standardized (β) partial regression coefficients were also calculated to help assess the relative importance of the predictor variables in each regression model (Zar 1999).

Growth projections under climate change scenarios

Projections of climate change under two different IPCC (2001) emission scenarios (A2 and B2) (Flato and Boer 2001) were obtained for each of the 65 sites using the program ClimatePP (version 3.0) (Wang et al. 2006) for three future periods in the 21st century (2010-2039, 2040-2069, and 2070-2099) in the same manner as described in Chapter III (p. 56). Further descriptions of ClimatePP and the general conditions underlying the two emission scenarios are also provided in Chapter III (p. 56). Changes in BH_{BAI}, AB_{VI}, and US_{VI} for each ER was projected for the three future periods based on applying separately the regression models for TAV and CMI to the future climate scenarios. The significance of the projected growth estimates were determined using the same procedure described in Chapter III (p. 57).

Results

Growth characteristics

The percentage of missing rings was greatest at SH and fewest at US versus the other positions and portions of the stem (BH, AB) for each ER and for all ERs combined (Table 4-2). Similarly, mean sensitivity of the regional chronologies was the greatest for SH_{BAI} for each ER and for all ERs combined (Table 4-2). For all ERs combined, mean sensitivity of BH_{BAI} was greater than for US_{VI}.

BH_{BAI} was strongly and positively correlated with SH_{BAI} and AB_{VI} for each ER and for all ERs combined (all $p < 0.01$) (Table 4-3). By comparison, the strength of the correlation was weaker between BH_{BAI} and US_{VI} but was still significant (all $p < 0.01$).

BH_{BAI} was also positively correlated with BH_{RI} (all $p < 0.01$). The chronologies of the growth index variables for all elevational regions combined are presented in Fig. 4-2.

Growth-climate relationships

The prediction sum of squares (PRESS) were reasonably close to the error sum of squares (SSE) which lends support to the validity of the regression models (Kutner et al. 2004) (Appendix II). Responses of SH_{BAI} growth chronologies to temperature and moisture index were very similar to the corresponding BH_{BAI} growth chronologies for each of the ER and for all ERs combined (not presented). BH_{BAI} growth responded negatively to high summer temperatures in the year prior to ring formation (t-1) in each ER, and this growth response to climate was also the most influential factor for all ERs combined [i.e., T1_aug(t-1)] according to the ranking of the absolute values of the β regression coefficients (Table 4-4; Fig. 4-3). For all ERs combined and in HL, BH_{BAI} growth responded positively to the 7-month period of October (t-1) to April (t) [T7_oct(t-1)_apr(t)] while BH_{BAI} in the other ER responded to portions of this 7-month temperature period. Responses of AB_{VI} growth were generally similar to corresponding BH_{BAI} except for the additional negative association with summer (t) temperature [T2_may(t)_jun(t)] in each ER and for all ERs combined. In contrast to BH_{BAI}, US_{VI} and BH_{RI} responded primarily to summer (t) temperature in most of the ER and for all ERs combined [T1_jun(t)]. For most of the ER and for all ERs combined, BH_{RI} responded secondarily and negatively to summer temperature in the prior year.

Except in HL, moisture variables generally explained less variance in growth than did temperature (Fig. 4-3; Fig. 4-4). The most influential moisture variable affecting

BH_{BAI} growth in each of the ER and for all ERs combined [M1_aug(t-1)] was the effect of late summer (t-1) moisture stress. Compared to BH_{BAI}, AB_{VI} growth generally had similar relationships to climate in each of the ER; while in the generally drier ER (HL, CH) AB_{VI} as well as US_{VI} growth differed mainly in terms of the greater impact of moisture stress in the summer of the year of ring formation (t) [M2_may(t)_jun(t)]. In FH [M2_feb(t)_mar(t)], RM [M3_feb(t)_apr(t)] and for all ERs combined [M2_feb(t)_mar(t)], US_{VI} growth was primarily influenced by a negative relationship with late winter/early spring moisture. For all ERs combined, BH_{RI} was primarily and negatively associated with moisture conditions for the period of M4_oct(t-1)_jan(t).

Growth projections under climate change scenarios

The climate conditions under the two climate change scenarios are shown in Chapter III (Table 3-6). The relative pattern of changes in projected growth through the three future periods (2010-2039, 2040-2069, 2070-2099) were similar between the climate change scenarios (A2 and B2) except that the magnitude of the changes were generally greater under the A2 scenario (Fig. 4-5; Fig. 4-6). For the temperature based projections, the magnitude of the projected declines in growth in FH, CH and for all ERs combined were more pronounced for AB_{VI} versus BH_{BAI} for either scenario and especially by the last projected period (2070-2099). Relative to the temperature based projections, the projected changes in growth were generally less pronounced for the moisture based projections, in which the projected declines in growth were only significant for the generally drier ER (HL, CH). Under the temperature models and for

the last projected period in particular, some of the growth projections were based on temperature conditions outside the range of initial model development.

Discussion

Although interannual growth variation in the upper stem was positively correlated with that recorded in the lower stem, there were distinct differences in the observed responses to climate variables. At breast height, stem growth was most negatively affected by warm, dry conditions in late summer of the previous year. In contrast, the results of this study supported the hypothesis that growth higher up the stem is principally affected by climatic conditions during the period of ring formation (Fritts 1976). The principal temperature response of upper stem growth was the negative effect of heat stress in the early summer of the current year. This climatic response pattern was reinforced by the direct relationship between the ratio of breast height to upper stem growth (BH_{RI}) and higher than average temperature in the early summer of the current growing season, which suggested that heat stress limits relative carbon allocation to the upper stem. These results are consistent with general phenological patterns of carbon allocation in conifers. That is, during the period of active crown and foliage growth in early summer, the upper stem of the crown region by being closer to the source of carbohydrate production, is a stronger carbon sink and receives higher priority for carbon allocation compared to the lower stem (Fritts 1976; Gower et al. 1995). Furthermore, rates of tree respiration is an important factor that determines the net amount of carbon available for partitioning to different tree organs (Gower et al. 1995; Lacointe 2000). Consequently, as supported by this study, high temperatures which lead to increased rates

of respiration can limit amount of available carbon for construction of new growth material.

The lagged growth response at breast height to climatic stress (heat stress and moisture stress) in late summer of year prior to ring formation seen in all ecoregions in this study is a general growth pattern not just confined to lodgepole pine (Chhin et al. 2008) but has also been widely observed for other northern pines and as well as spruces in North America (Fritts 1976; Kozlowski et al. 1991). The response of the ratio of breast height to upper stem growth to climate in this lagged seasonal window also indicated that heat and moisture stress limits allocation to the lower stem. By late summer after active crown growth, carbon is generally allocated more to bud set and accumulation of carbohydrate reserves, which as this study supports, is an important driver of growth of the lower stem in the following growing season (Fritts 1976; Kozlowski et al. 1991; Gower et al. 1995). These results reinforce the general understanding that growth at lower sections in the bole in lodgepole pine is primarily affected by climatic conditions in the months and seasons prior to the start of the growing season of ring formation (Fritts 1976).

It was confirmed in this study that interannual variation in volume increment of the whole stem (AB_{VI}) was highly correlated with growth at breast height. Basal area increment at breast height was also highly correlated with whole stem annual volume increment in red spruce (*Picea rubens* Sarg.) (LeBlanc 1990), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws) (Arbaugh and Peterson 1993), European beech (*Fagus sylvatica* L.) (Bouriaud et al. 2005), and Turkey oak (*Quercus cerris* L.) (Corona et al. 1995). In the current study, however, whole stem growth was more influenced by

climatic conditions in the growing season in the year of ring formation compared to growth at breast height. In all ecoregions, whole stem growth was negatively affected by higher than average temperatures in the summer of the current year whereas corresponding growth at breast height was not affected by temperatures during this seasonal window. Corona et al. (1995) found similar results for Turkey oak and observed that compared to breast height, whole stem climatic responses were markedly more affected by precipitation conditions in July of the year of ring formation. The results indicate that while strong allometric relationships between breast height and whole stem growth may suggest similar responses to climate, these assumptions should be carefully considered by explicitly examining the response to climate for all measures of growth.

The structure of the basal area index-growth chronology at breast height was highly correlated to that at stump height and the responses to climate were also generally similar; this was despite the fact that the percentage of missing rings and the degree of interannual growth variability as measured by mean sensitivity were greater at stump height versus breast height. The high correlation was also observed for white spruce (*Picea glauca* Moench (Voss)) at its southern limit of distribution in south-western Manitoba (Chhin and Wang 2005). For tree species such as white spruce with a slow juvenile growth phase and consequently a greater difference in the number of annual rings between breast height and stump height, there is greater justification to use growth chronologies from stump height, with their longer temporal sequence. However, for tree species with fast juvenile growth rates it may not be a worthwhile investment to sample below breast height for most applications; for lodgepole pine in this study there was only a difference of 5 years between breast and stump height.

The differences in climatic response between different positions and portions of the stem also translated into different forecasted estimates of growth under the future climate change scenarios. In particular, the projected growth decline in response to climatic warming was generally more pronounced for the whole stem versus estimates from breast height only. The growth projections indicated that the drier ecoregions (Boreal Highlands, Cypress Hills) will be vulnerable to declines in growth induced by future increases in dryness. There were consistent declines in growth in the last projected period of the 21st century in the foothills region regardless of growth variable and under either climate scenario in response to climatic warming. This is disconcerting since the foothills region represents the main distributional range of lodgepole pine in Alberta. Consequently, the projected growth declines in the foothills could affect future timber supply in the province as well as the ecological integrity of other forest values (e.g., wildlife habitats and biodiversity).

References

Alberta Land and Forest Service. 1994. Permanent sample plot field procedures manual. Timber Management Branch, Alberta Forest Service, Edmonton, Alberta. Pub. FMOPC 83-03.

Arbaugh, M.J., and Peterson, D.L. 1993. Stemwood production patterns in ponderosa pine: effects of stand dynamics and other factors. Pacific Southwest Research Station, USDA Forest Service, Washington. Research Paper PSW-RP-217.

Bascietto, M., and Scarascia-Mugnozza, G. 2004. A collection of functions to determine annual tree carbon increment via stem-analysis. Annals of Forest Science, **61**: 597-602.

Bouriaud, O., Breda, N., Dupouey, J.L., and Granier, A. 2005. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. Canadian Journal of Forest Research, **35**: 2920-2933.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Chhin, S., Hogg, E.H., Lieffers, V.J., and Huang, S. 2008. Influences of climate on the radial growth of lodgepole pine in Alberta. Botany, **86**: 167-178.

Chhin, S., and Wang, G.G. 2005. The effect of sampling height on dendroclimatic analysis. Dendrochronologia, **23**: 47-55.

Clyde, M.A., and Titus, S.J. 1987. Radial and longitudinal variation in stem diameter increment of lodgepole pine, white spruce, and black spruce: species and crown class differences. Canadian Journal of Forest Research, **17**: 1223-1227.

Corona, P., Romagnoli, M., and Torrini, L. 1995. Stem annual increments as ecobiological indicators in Turkey oak (*Quercus cerris* L.). Trees, **10**: 13-19.

Douglass, A.E. 1920. Evidence of climatic effects in the annual rings of trees. Ecology, **1**: 24-32.

Duff, G.H., and Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species. I. Then controls of cambial and apical activity in *Pinus resinosa* Ait. Canadian Journal of Botany, **31**: 471-513.

Duff, G.H., and Nolan, N.J. 1957. Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in *Pinus resinosa* Ait. Canadian Journal of Botany, **35**: 527-572.

Fayle, D.C.F., and MacDonald, G.B. 1977. Growth and development of sugar maple as revealed by stem analysis. Canadian Journal of Forest Research, **7**: 526-536.

Flato, G.M., and Boer, G.J. 2001. Warming asymmetry in climate change simulations. Geophysical Research Letters, **28**: 195-198

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, UK.

Gower, S.T., Isebrands, J.G., and Sheriff, D.W. 1995. Carbon allocation and accumulation in conifers. *In* Resource physiology of conifers. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 217-254.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research, **57**: 205-221.

Hennigar, C.R., MacLean, D.A., and Norfolk, C.J. 2007. Effects of gypsy moth defoliation on softwood and hardwood growth and mortality in New Brunswick, Canada. Northern Journal of Applied Forestry, **24**: 138-145.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology, **84**: 115-122.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research, **35**: 610-622.

Hutchinson, M.F. 2000. ANUSPLIN Version 4.1 User Guide. Centre for Resource and Environmental Studies, Australian National University, Canberra ACT 0200, Australia.

IPCC. 2001. Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson. Cambridge University Press, Cambridge, UK.

Jones, P.D., and Hulme, M. 1996. Calculating regional climatic time series for temperature and precipitation: methods and illustrations. International Journal of Climatology, **16**: 361-377.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.

Kutner, M.H., Nachtsheim, C.J., Neter, J., and Li, W. 2004. Applied linear statistical models. 5th ed. McGraw-Hill, New York, NY.

Lacointe, A. 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. Annals of Forest Science, **57**: 521-533.

LeBlanc, D.C. 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Canadian Journal of Forest Research, **20**: 1399-1407.

Makinen, H., Nojd, P., and Isomaki, A. 2002. Radial, height and volume increment variation in *Picea abies* (L.) Karst. stands with varying thinning intensities. Scandinavian Journal of Forest Research, **17**: 304-316.

McKenney, D.W., Hutchinson, M.F., Kesteven, J., and Venier, L. 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Canadian Journal of Plant Science, **81**: 129-143

Meng, S.X., Lieffers, V.J., Reid, D.E.B., Rudnicki, M., Silins, U., and Jin, M. 2006. Reducing stem bending increases the height growth of tall pines. Journal of Experimental Botany, **57**: 3175-3182.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Government of Alberta. Pub. No. T/852.

Schweingruber, F.H., Kairiukstis, L., and Shiyatov, S. 1990. Sample selection. *In* Methods of dendrochronology: Applications in the environmental sciences. *Edited by* E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 95-129.

Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. The University of Arizona Press, Tuscon.

Tasissa, G., and Burkhart, H.E. 1997. Modeling thinning effects on ring width distribution in loblolly pine (*Pinus taeda*). Canadian Journal of Forest Research, **27**: 1291-1301.

Varem-Sanders, T.M.L., and Campbell, I.D. 1996. DendroScan: a tree-ring width and density measurement system. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta. Spec. Rep. 10.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York, NY.

Wang T., Hamann, A., Spittlehouse, D.L., and Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. International Journal of Climatology, **26**: 383-397.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research, **21**: 414-416.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, NJ.

Table 4-1. Sampling characteristics of the elevational ecoregions.

	HL[1]	FH	CH	RM	ALL
No. sites	13	36	4	12	65
No. trees	77	216	24	72	389
No. disks	847	2376	264	792	4279

[1] Elevational region (ER) abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ALL, all ERs combined

Table 4-2. Characteristics of chronologies of growth variables across elevational ecoregions.

	HL	FH	CH	RM	ALL
Mean chronology start date					
SH_{BAI}	1912	1906	1881	1906	1906
BH_{BAI}	1916	1912	1884	1913	1911
AB_{VI}	1916	1912	1884	1913	1911
US_{VI}	1944	1943	1918	1946	1942
Missing rings (%)					
SH	0.056	0.192	0.844	0.184	0.216
BH	0.037	0.130	0.730	0.076	0.150
AB	0.042	0.101	0.513	0.065	0.117
US	0.027	0.062	0.327	0.054	0.077
Mean sensitivity					
SH_{BAI}	0.130	0.112	0.202	0.125	0.106
BH_{BAI}	0.108	0.095	0.165	0.102	0.091
AB_{VI}	0.085	0.077	0.157	0.093	0.076
US_{VI}	0.106	0.071	0.162	0.102	0.072

Note: See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables.

Table 4-3. Pearson correlation coefficient (r) between basal area index growth at breast height (BH_{BAI}) and growth variables at other positions of the stem across elevational ecoregions.

BH_{BAI} vs. growth variables	HL	FH	CH	RM	ALL
SH_{BAI}	0.953	0.956	0.942	0.952	0.969
AB_{VI}	0.772	0.894	0.935	0.904	0.901
US_{VI}	0.407	0.648	0.829	0.655	0.685
BH_{RI}	0.625	0.623	0.481	0.379	0.558

Note: All r significant at $p < 0.01$. See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables.

Table 4-4. Coefficients of regression models relating growth variables (GV) at different positions and portions of the stem with climate variables across elevational regions (ERs).

	Mean temperature					Climate moisture index			
ER/GV	C	V1	V2	V3	V4	C	V1	V2	V3
HL									
BH_{BAI}	0.995	0.520	-0.368			1.000	0.457	-0.432	0.256
		(0.0240)	(0.0437)				(0.0049)	(0.0064)	(0.0078)
AB_{VI}	0.995	0.466	-0.357			0.996	0.653	-0.427	0.282
		(0.0117)	(0.0280)				(0.0100)	(0.0084)	(0.0061)
US_{VI}	0.994	-0.618	0.430	0.281		1.001	0.590	0.248	
		(0.0496)	(0.0128)	(0.0149)			(0.0092)	(0.0086)	
BH_{RI}	0.994	0.465	-0.347	0.276		0.996	-0.543	-0.434	0.262
		(0.0575)	(0.0426)	(0.0058)			(0.0067)	(0.0200)	(0.0031)
FH									
BH_{BAI}	0.997	-0.511	0.349			1.000	0.474	-0.291	
		(0.042)	(0.0147)				(0.0086)	(0.0050)	
AB_{VI}	0.997	0.593	-0.417	-0.400		1.000	0.345	-0.293	
		(0.0231)	(0.0240)	(0.0307)			(0.0052)	(0.0042)	
US_{VI}	0.993	-0.515	0.413			0.998	-0.316	0.265	
		(0.0297)	(0.01490)				(0.0102)	(0.0024)	
BH_{RI}	1.001	0.511	-0.464			0.997	0.352	-0.306	
		(0.0277)	(0.0180)				(0.0047)	(0.0072)	
CH									
BH_{BAI}	0.990	0.501	-0.459	-0.302		0.975	0.431	0.344	-0.274
		(0.018)	(0.0375)	(0.0208)			(0.0101)	(0.0117)	(0.0346)
AB_{VI}	0.988	0.466	-0.458	-0.308		0.981	0.386	0.297	-0.288
		(0.0214)	(0.0421)	(0.0370)			(0.0096)	(0.0062)	(0.0185)
US_{VI}	0.986	-0.372	0.305			0.987	0.285		
		(0.0362)	(0.0177)				(0.0073)		
BH_{RI}	0.985	0.395	0.256			0.995	0.339		
		(0.0098)	(0.0129)				(0.0052)		
RM									
BH_{BAI}	0.995	-0.491	0.309	0.275		0.996	0.472	-0.281	
		(0.0257)	(0.0144)	(0.0124)			(0.0083)	(0.0067)	
AB_{VI}	0.992	0.503	-0.477	-0.324	0.287	0.996	0.415	-0.366	
		(0.0200)	(0.0232)	(0.0266)	(0.0071)		(0.0068)	(0.0081)	
US_{VI}	0.997	-0.324	0.323	-0.315		1.003	-0.406		
		(0.0170)	(0.0136)	(0.0221)			(0.0063)		
BH_{RI}	0.998	0.560	-0.372	0.249		0.991	-0.430	0.274	
		(0.0297)	(0.0268)	(0.0074)			(0.0096)	(0.0024)	
ALL									
BH_{BAI}	0.994	-0.505	0.397			0.997	0.447	-0.323	
		(0.0262)	(0.0181)				(0.0086)	(0.0059)	
AB_{VI}	0.995	0.589	-0.432	-0.387		0.998	0.401	-0.346	
		(0.023)	(0.0308)	(0.0298)			(0.0066)	(0.0118)	
US_{VI}	0.994	-0.523	0.412	-0.248		0.996	-0.358	0.274	
		(0.0314)	(0.0153)	(0.0168)			(0.0116)	(0.0051)	
BH_{RI}	0.997	0.494	-0.432	0.243		0.998	-0.347	0.296	
		(0.0266)	(0.0329)	(0.0061)			(0.0054)	(0.0042)	

Note: The first term in the regression model is the constant (C). The regression terms (V1-V4) are listed in descending order according to the ranking of the absolute values of the standardized (β) regression coefficients (Zar 1999), and values in parentheses represent the corresponding partial regression coefficients (cf. Fig.4-3 and Fig. 4-4). See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables.

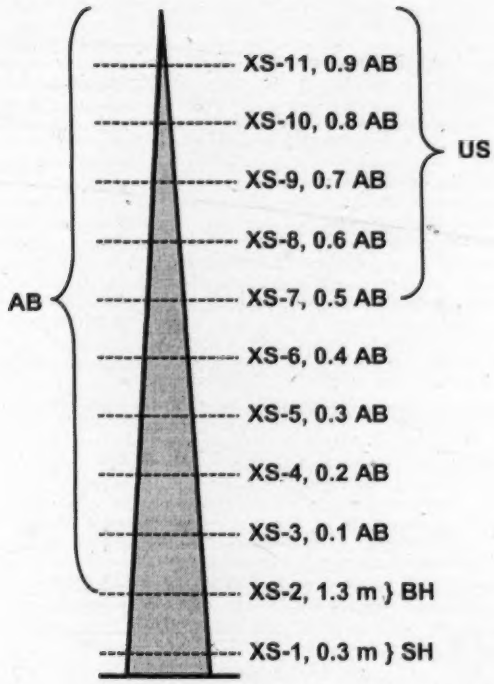

Figure 4-1. Diagrammatic representation of the methodology for the serial sectioning of lodgepole pine stems. Cross-sectional (XS) disks were sampled at 11 positions along the stem of each tree which first included: XS-1, 0.3 m (stump height (SH)); and XS-2, 1.3 m (breast height (BH)). The remaining 9 disks were obtained along equally spaced points from the portion of the tree stem between breast height to the top of the tree (i.e., tree height above breast height (AB) = total tree height – 1.3 m). The upper stem (US) portion includes XS-7, XS-8, XS-9, XS-10 and XS-11.

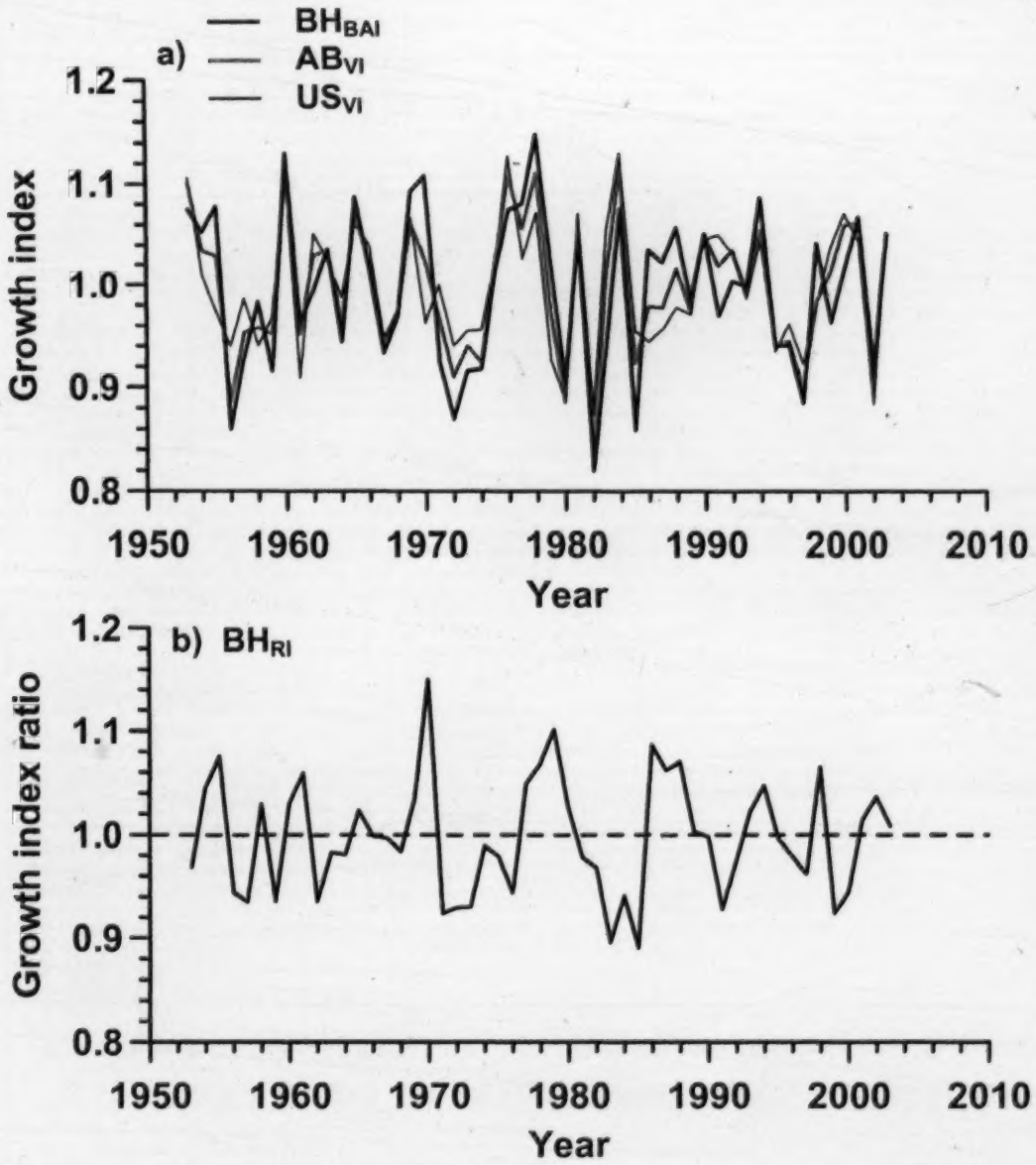

Figure 4-2. For all regions combined: (a) Growth variables based on cross-sections (XS) at different positions and portions of the stem (c.f. Figure 4-1): BH_{BAI}, basal area index growth at breast height (XS-2, 1.3 m); AB_{VI}, volume index growth for stem portion above breast height (all XS except XS-1); US_{VI}, volume index growth of upper stem (includes XS-7, XS-8, XS-9, XS-10 and XS-11). (b) BH_{RI}, growth index ratio of BH_{BA} (basal area growth at breast height) to US_{BA} (average basal area growth of upper stem).

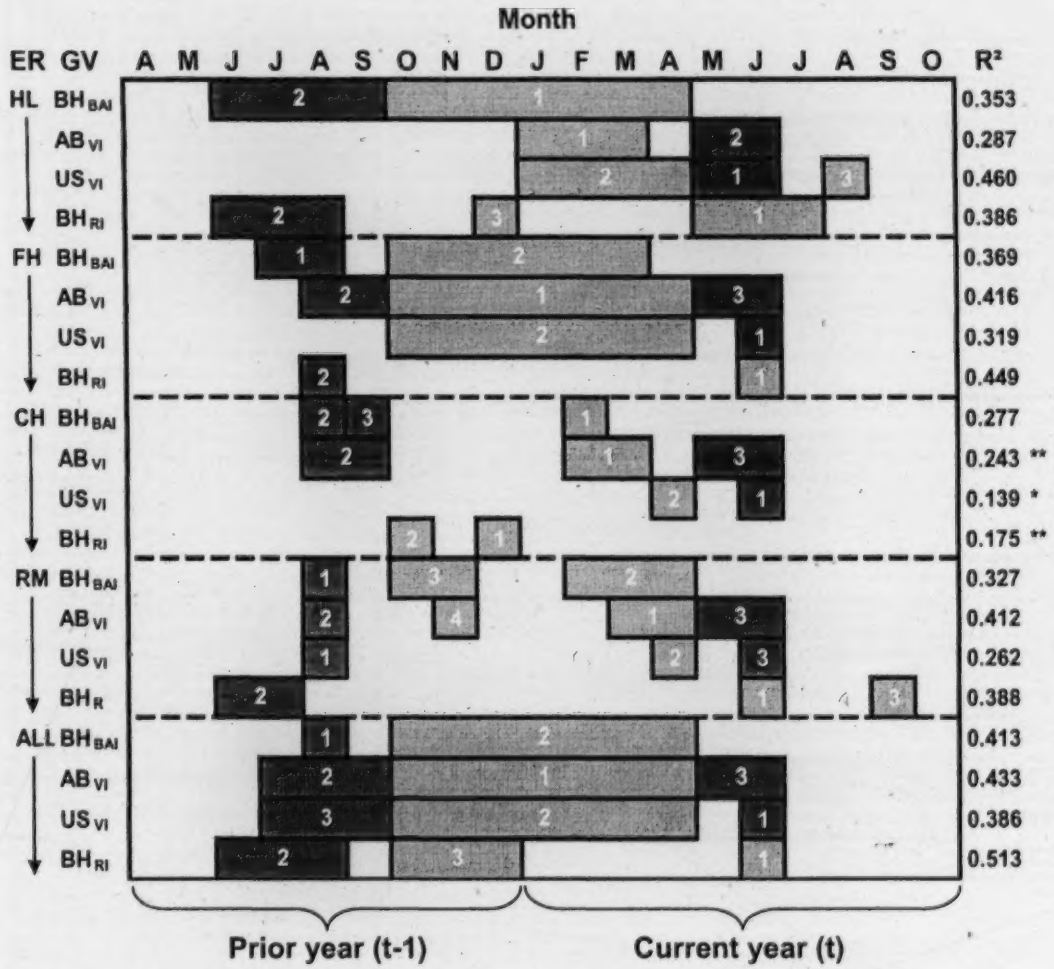
Month
ER GV A M J J A S O N D J F M A M J J A S O R²
HL BH BAI 0.353
AB VI 0.287
US VI 0.460
BH RI 0.386
FH BH BAI 0.369
AB VI 0.416
US VI 0.319
BH RI 0.449
CH BH BAI 0.277
AB VI 0.243 **
US VI 0.139 *
BH RI 0.175 **
RM BH BAI 0.327
AB VI 0.412
US VI 0.262
BH R 0.388
ALL BH BAI 0.413
AB VI 0.433
US VI 0.386
BH RI 0.513
Prior year (t-1)
Current year (t)

Figure 4-3. Regression models relating growth variables (GV) at different positions and portions of the stem with temperature variables across elevational regions (ERs). For Figs. 4-3 and 4-4, the regression analysis was conducted over two growing seasons from April of the prior year (t-1) to October of the current year (t). For each regression model, predictor climate variables having a positive relationship with growth are denoted by light gray boxes; and predictor climate variables having a negative relationship with growth are denoted by darker gray. Predictor variables are also ranked according to the absolute value of their standardized (β) regression coefficient (Zar 1999); a rank of 1 denotes the predictor variable with the highest β coefficient. The predictor variables are referred to accordingly in the text: e.g., For temperature responses in HL at BH_{BAI}, the predictor variables are abbreviated as T4_jun(t-1)_sep(t-1) and T7_oct(t-1)_apr(t). All regression models are statistically significant at $p < 0.001$ unless otherwise indicated (*, $p < 0.05$; **, $p < 0.01$). Coefficients of regression models are listed in Table 4-4. See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables.

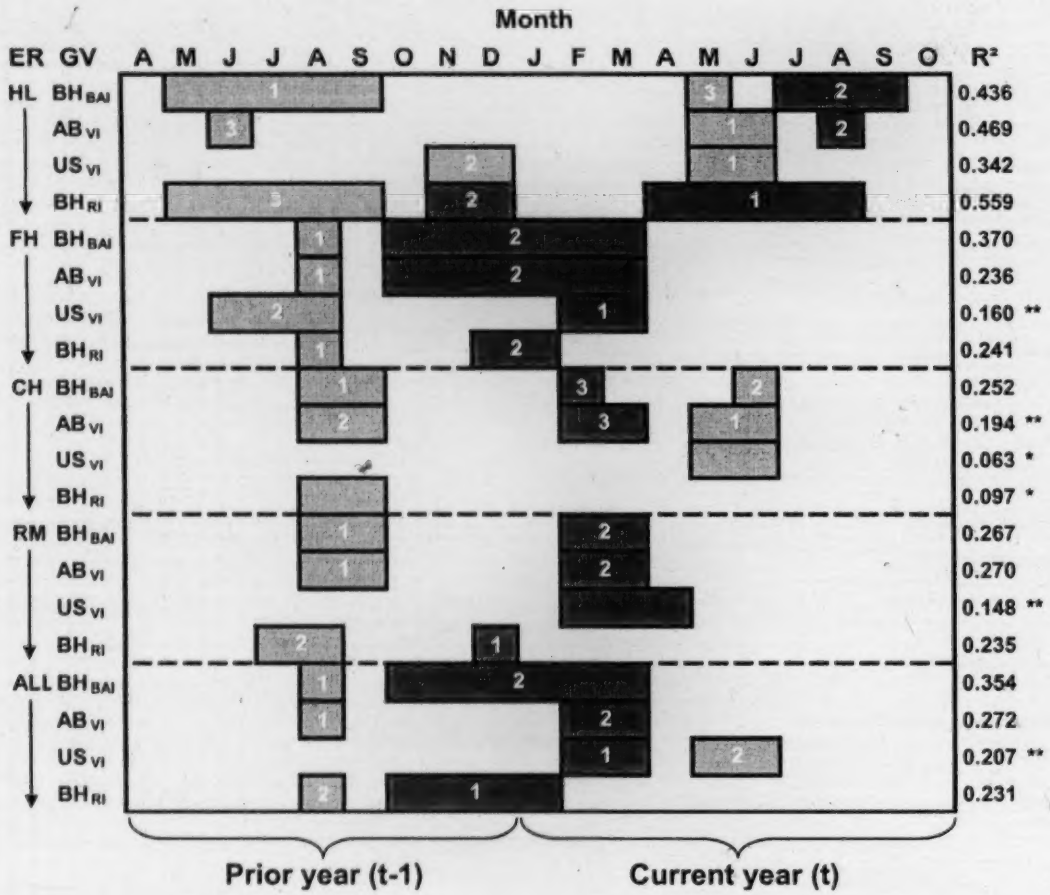
Month
ER GV A M J J A S O N D J F M A M J J A S O R²
HL BH BAI 0.436
AB VI 0.469
US VI 0.342
BH RI 0.559
FH BH BAI 0.370
AB VI 0.236
US VI 0.160 **
BH RI 0.241
CH BH BAI 0.252
AB VI 0.194 **
US VI 0.063 *
BH RI 0.097 *
RM BH BAI 0.267
AB VI 0.270
US VI 0.148 **
BH RI 0.235
ALL BH BAI 0.354
AB VI 0.272
US VI 0.207 **
BH RI 0.231
Prior year (t-1)
Current year (t)

Figure 4-4. Regression models relating growth variables (GV) at different positions and portions of the stem with moisture variables across elevational regions (ERs). See Figure 4-3 caption but variables lead with the letter M.

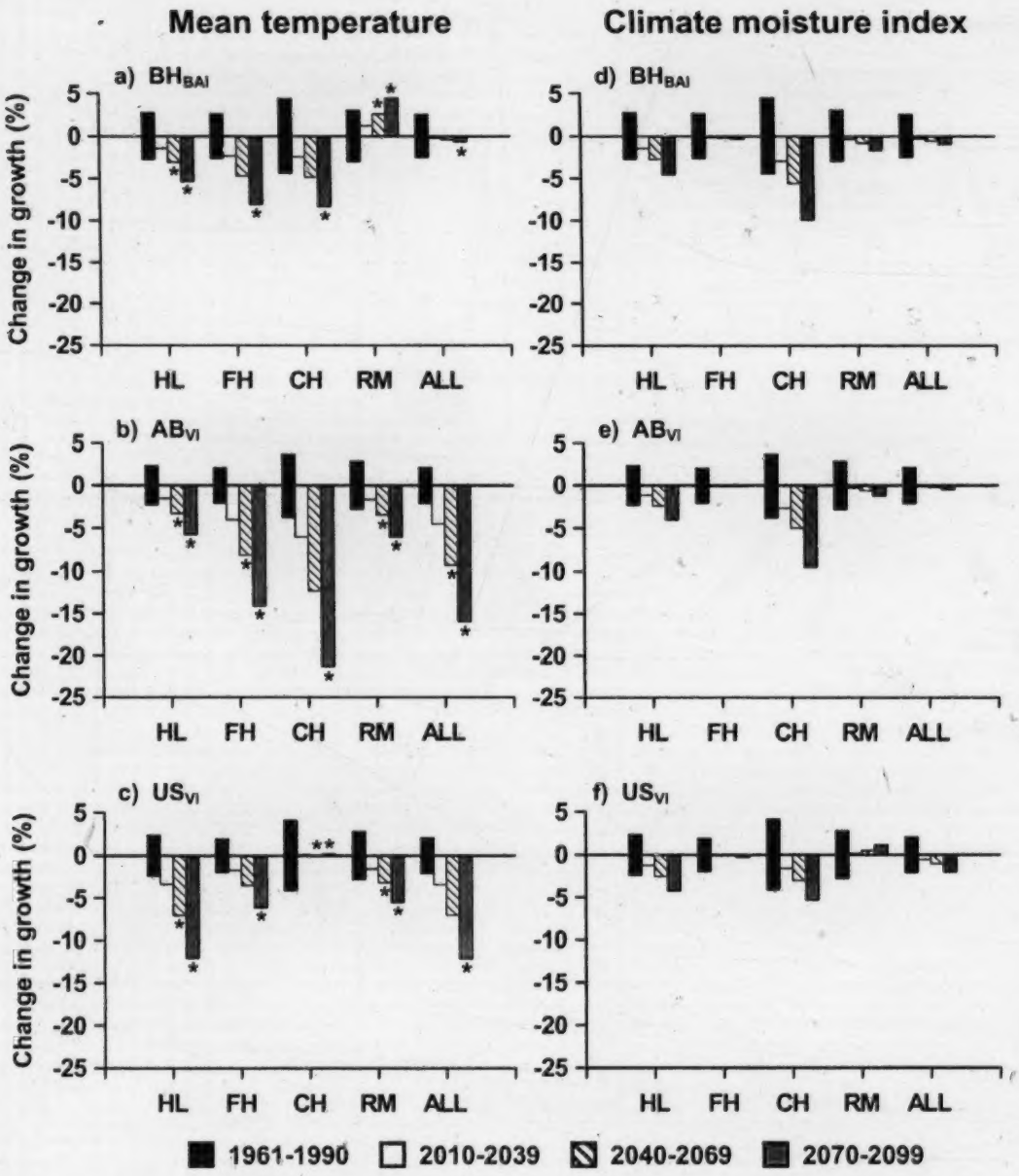

Figure 4-5. Projections of growth variables across elevational ecoregions for 3 future periods in the 21st century under the A2 climate change scenario. The projected estimates are based on applying separately the regression models for temperature (TAV, Fig. 4-3) and moisture index (CMI, Fig. 4-4) to the future climate scenarios. The lower and upper limits of a 95% confidence interval of the mean for the control period (1961-1990) and growth projections for the climate scenario periods are expressed as percentage change relative to the mean growth for the control period. See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables. Asterisks indicate that growth is projected for a period in which at least one of the climate variables is outside the range of initial model development.

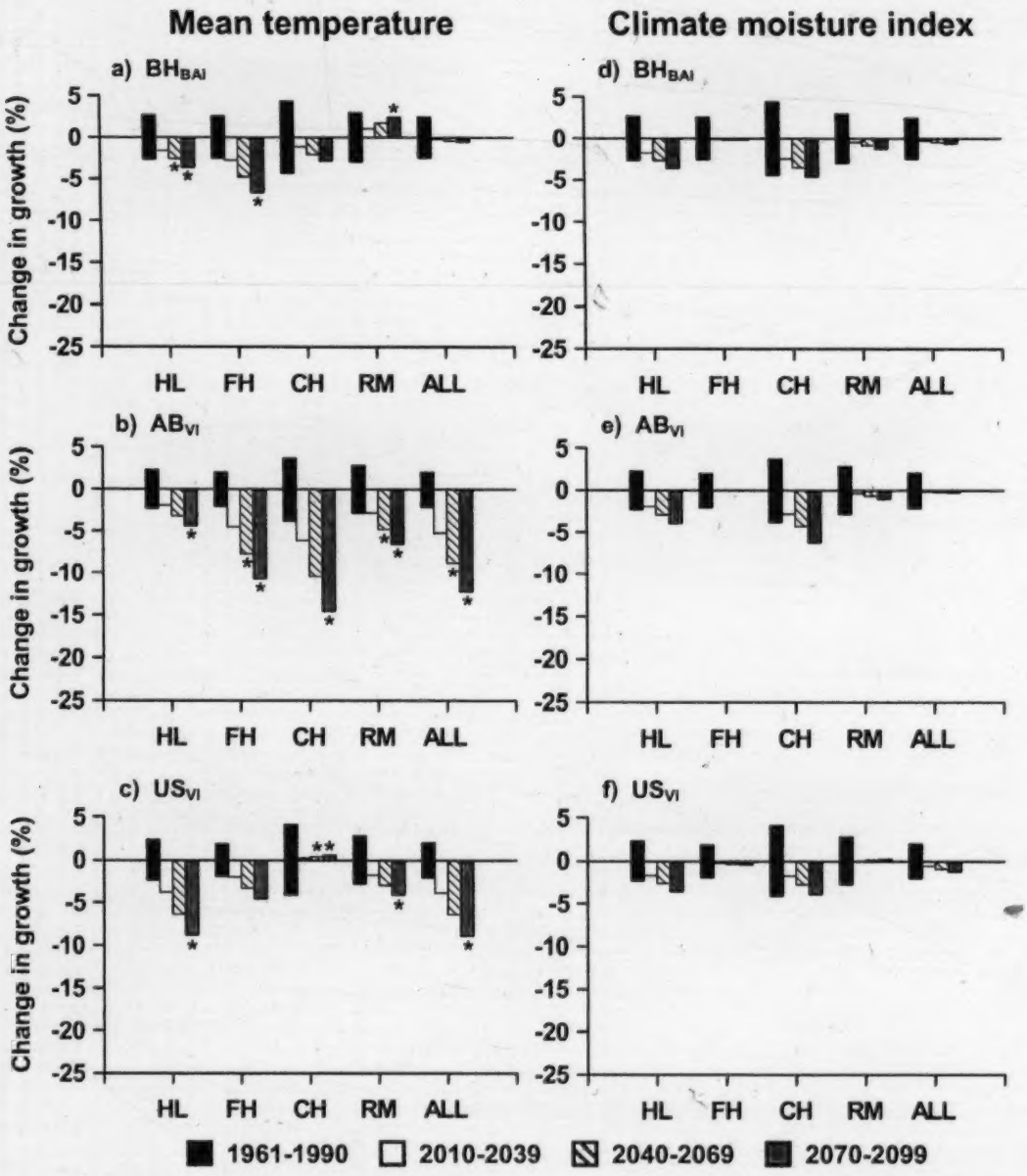

Figure 4-6. Projections of growth variables across elevational ecoregions for 3 future periods in the 21st century under the B2 climate change scenario. See Fig. 4-5 caption.

Chapter V: General Discussion and Conclusions

This dissertation retrospectively examined growth-climate relationships in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in the cordilleran forests of Alberta. The historical relationships between growth and climate over the last century were used to project future growth under different scenarios of climate change. Specifically, the following research objectives were examined:

1) Identify the principal climatic factors that have affected the historical pattern of growth of lodgepole pine stands in the cordilleran forest region of Alberta
2) Examine whether growth-climate relationships vary among ecological regions within the cordilleran forest
3) Determine whether growth-climate relationships differ among different diameter size classes of lodgepole pine
4) Examine whether growth-climate relationships derived at the traditional breast height are representative of growth responses to climate of other portions of the tree stem
5) Assess the potential impacts of future climate scenarios on growth projections of lodgepole pine in the 21st century

Historical Growth-Climate Relationships

Chapter II represents the first regional-scale analysis of lodgepole pine radial growth variation in relation to climate in North America. In this chapter, the radial growth-climate relationships that were identified indicate that cool and moist conditions

in late summer of the previous growing season led to better radial growth during the following year. Warm and dry winters and springs, and warm conditions in the autumn of the year of ring formation, also promoted ring growth. These growth-climate relationships were examined in light of inferred ecophysiological mechanisms (Kozlowski et al. 1991; Fritts 1976). The lag in response to climatic stress was likely due to the role of carbohydrate reserves and the multi-year development of buds and foliage. Possible ecophysiological stresses occurring during winter dormancy were also proposed (Havrenak and Tranquillini 1995).

In Chapter III, similar to the growth-climate relationships identified in Chapter II, basal area growth of lodgepole pine was generally sensitive to a lag in response to heat and moisture stress in late summer, the degree of winter harshness, and the timing of the start of the growing season. In contrast to the study in Chapter II which is limited to a sparser network of 17 sites, the main contribution of the study in Chapter III is that it answered whether growth responses to climate varied by ecological region and among diameter size classes over a broader spatial network of 65 sites. Growth-climate relationships varied by ecological region since growth was inhibited by low temperature in all winter months at the most northern Boreal Highland sites which had the coldest winters. However, this effect was interrupted in some of the midwinter months in the more southerly sites in the Rocky Mountains, and it was postulated that this could be due to the damaging influences of Chinook winds. All ecological regions responded to the timing of the start of the growing season, except in Cypress Hills, which already had the warmest temperatures such that the spring heat units needed to resume growth were easily met. There was a strong correlation in interannual growth patterns between the

largest trees with the trees from the other diameter classes, and trees of all diameter classes generally responded to climate in the same way. This indicates that it is sufficient to sample only the largest diameter lodgepole pine trees in a stand to provide insight into growth-climate relationships.

The study in Chapter IV of the dissertation explicitly examined growth-climate relationships of the upper and lower portions of tree stems and found support for the hypothesis that growth of the upper stem is controlled mainly by climatic factors in the year of ring formation. The results in this chapter also reinforced the general understanding that growth at breast height in lodgepole pine is controlled primarily by climatic factors in the year prior to ring formation. Thus, there were clear differences in growth responses to climate at different heights along the stem, so that relationships obtained from breast height samples are not representative of volume growth responses of the whole stem. The conceptual and theoretical framework underpinning seasonal patterns of carbon allocation (Fritts 1976; Gower et al. 1995; Lacointe 2000) which helped explain the differential growth responses to climate along the bole is not new, but needs wider exposure in the dendrochronological research community.

Radial and height growth (Monserud et al. 2006) of lodgepole pine in Alberta respond favourably to warm springs. Studies that utilize site index cannot examine possible relationships between how growth in the current year is affected by climatic conditions of the previous growing season. In contrast, this dissertation (Chapters II, III, IV) provided novel insight into the strong conditioning influence of lagged-climatic factors in late summer of the year prior to ring formation.

Potential Effects of Future Climate Change

Future changes in lodgepole pine productivity were estimated by applying climate change scenario projections to growth-climate equations obtained from the retrospective analyses of tree-rings. Based on this approach, lodgepole pine productivity is expected to decline by 5 to 6% in response to climatic warming in Alberta later this century (2070-2099) relative to 1961-1990, along its main distributional range in the foothills (Chapter III). Furthermore, the forecasted decline in the foothills due to climatic warming was more pronounced for whole stem projections (11 to 14%) versus those based at breast height (7 to 8%) (Chapter IV). The projected growth declines in the foothills could affect future timber supply in the province as well as the ecological integrity of other forest values (e.g., watershed health, wildlife habitats and biodiversity). However, there are uncertainties in the projected declines related to uncertainties in projected changes in precipitation, and the undetermined net effect of other positive and negative factors which will likely interact with climate change to affect future forest productivity (Loehle and LeBlanc 1996; Hogg and Bernier 2005).

Potential losses in lodgepole pine forest cover can be buffered by changes in species composition which in turn depends on factors such as the rates of seed dispersal and migration of competing tree species. The decline in productivity of lodgepole pine in the foothills under climate change could open the door to competitive displacement by other tree species more adapted to the new climate (Loehle 2003), such as trembling aspen (*Populus tremuloides* Michx) which is present at lower elevations in the foothills (Natural Regions Committee 2006). Assisted migration of lodgepole pine using optimized seed sources from warmer climatic zones could be an adaptive measure in the

context of climate change (Wang et al. 2006), although realistically, this might be only logistically feasible for a limited number of sites (Spittlehouse 2005). Assisted migration of other drought and heat tolerant conifers such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and in particular ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) could serve as other potential tree candidates for assisted migration (Kolb and Robberecht 1996; Watson and Luckman 2002).

Other physical aspects of environmental change can buffer the severity of the projected growth declines (Hogg and Bernier 2005). The increasing trend in atmospheric CO_2 concentration could increase forest productivity through a CO_2 fertilization effect. Especially in water-limited regions, increased CO_2 concentration can lead to water-use efficiency (Wang et al. 2006). Anthropogenically-induced increases in atmospheric nitrogen deposition could also offset the projected growth declines.

Climate-induced changes in disturbance regimes (fire and insects) could accelerate losses in forest cover (Volney and Fleming 2000; Flannigan et al. 2001). Climatic warming could increase fire frequency which would likely favour fire-adapted, early successional trees species such as lodgepole pine and trembling aspen. Theoretical models of forest decline indicate that climate (e.g., climate warming) and severe weather events (e.g., drought) are important predisposing and inciting factors in tree mortality; however, insects are also an important but contributing factor to final tree mortality (Manion 1991). Hot and dry summers which facilitate mountain pine beetle (*Dendroctonus ponderosae* Hopk.) reproduction and mild winters that increase overwintering survival of beetle offspring have contributed to the epidemic scale populations of mountain pine beetle infesting and killing stands of lodgepole pine in

central British Columbia (Caroll et al. 2006). The area of climatically suitable habitats for the mountain pine beetle is expected to expand under future climate change (Caroll et al. 2006). Indeed, the mountain pine beetle has already recently expanded its range eastward into Alberta from central British Columbia and therefore poses a serious risk to the health and productivity of lodgepole pine forests in Alberta in the 21st century under climate change. The degree to which milder winters under climate change will translate into increased growth of lodgepole pine will depend on the magnitude of increased overwintering survival of mountain pine beetle populations. It was identified in this dissertation that hot and dry summers negatively affect lodgepole pine growth. These climatic conditions also promote mountain pine beetle development which could have an even larger impact on forest-level productivity as the direct effects of the climate on growth.

In addition to the looming role of the mountain pine beetle on future health and productivity of lodgepole pine forests, there can be other factors which lead to an upper limit to the benefits of milder winters and longer growing seasons. Excessively warm winters compromise a tree's ability to achieve and maintain maximal levels of cold hardiness (Ogren 2001; Hanninen et al. 2001). For instance, mild winters can lead to respiratory depletion of carbohydrate reserves including cryoprotective sugars, and this has been observed in seedlings of lodgepole pine which were experimentally over-wintered at higher temperatures (Ogren et al. 1997). Warmer winters are expected to lead to a greater incidence of thaw-freeze cycles which can promote cavitation of xylem (Sparks and Black 2000) and forest dieback (Auclair et al. 1996). Anomalously warm,

early springs can also be detrimental to growth since it would increase the likelihood of premature budburst and exposure to spring frost damage (Hanninen 2006).

Future Research Directions

Environmental change can affect interspecific biotic interactions (Loehle 2003; Brooker 2006). Examining multispecies responses to climate using dendrochronology in mixed forest stands will provide better insight into the potential role of interspecific, biotic interactions in shaping the species composition of forests under future climate change (Loehle 2003; Goldblum and Rigg 2005; Fonti et al. 2006; Pinto et al. 2007). While climate-productivity relationships have been examined in other tree species such as trembling aspen (*Populus tremuloides* Michx.) in vegetation zones outside the cordilleran forest region of Alberta (Hogg et al. 2005), further studies of aspen and other tree species should be examined within this forest region, particularly at lower elevations in the foothills where deciduous tree species are present (Natural Regions Committee 2006).

In contrast to numerous analyses of ring-width – climate relationships, less attention has been given to relationships between climate and other physical wood properties such as wood density, and chemical wood properties such as stable carbon isotope ratios ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) (D'Arrigo et al. 1992; Loader et al. 2003). Measuring interannual variations in wood density would provide insight into interannual variations in stem biomass increment (Bouriaud et al. 2005a). Stable carbon isotopes provide a record of how climatic conditions affect the uptake and fractionation of $^{13}CO_2$ via its affect on stomatal conductance and photosynthetic rates (McCarroll and Loader

2004). Stable carbon isotope analyses are usually conducted on cellulose which is extremely time-consuming to extract from tree rings (McCarroll and Loader 2004). Cellulose extraction is not required in some tree species, such that analyses can be conducted on milled whole wood samples which speeds up sample processing time (Loader et al. 2003). Although more costly to measure, annual variations in these other ring parameters could be examined to provide further insight into the climatic response pattern of lodgepole pine, as has been shown in other tree species (e.g., Barber et al. 2000; Gagen et al. 2006; Skomarkova et al. 2006).

Further studies of lodgepole pine using non-radioactive, isotopically labelled carbon could provide a more direct assessment of the role of carbohydrate reserves and carbon allocation patterns within the stem (Kagawa et al. 2005; Kagawa et al. 2006). Isotopic tracer studies of tree rings typically involve first applying a strong pulse of $^{13}CO_2$ to sealed branches or whole tree saplings. Subsequently, the concentration of $\delta^{13}C$ in tree rings is examined relative to natural baseline values (Kagawa et al. 2005; Kagawa et al. 2006). Differential growth responses along the stem could also be examined using point dendrometers placed at different heights of the stem in combination with data loggers recording seasonal weather parameters (Fritts 1976; Bouriaud et al. 2005b). That is, dendrometer based studies could provide insight into growth-climate relationships at the *intra*-annual scale. Nevertheless, dendrometer based studies face challenges with accounting for hourly and diurnal changes in shrinking and swelling of the tree stem (Zweifel et al. 2006). Further studies should also examine in other tree species how considering growth-climate relationships at other portions of the stem may affect the interpretation of climatic response patterns compared to that derived at the traditional

breast height. This may spur development of field equipment to sample the upper stem region that would be more cost-effective than aerial, hydraulic lifts for direct canopy access: e.g., some type of telescoping pole with an automatic, powered increment borer mounted on top.

This dissertation provided an indication of potential changes in future forest productivity but could not directly examine potential changes in distribution that can arise from forest dieback and tree mortality. Tree mortality is an important process of forest dynamics but mortality is a poorly understood process in ecology (Pedersen 1998). Thus, an essential area of further research that needs to be addressed is the examination of processes leading to mortality in lodgepole pine and other tree species that is not related to natural stand senescence. In particular, growth patterns in the decade or so preceding the year of death needs to be examined to determine the causes of death (climate, insects, etc.) (Pedersen 1998; Ogle et al. 2000; Suarez et al. 2004). Identification of a linkage between growth patterns preceding mortality would assist in the development of tree mortality prediction models (Bigler and Bugmann 2004; Das et al. 2007). Such models will be instrumental in more directly answering questions of potential distributional changes in forest cover that can arise due to potential forest dieback and decline under future climate change.

This dissertation focused on growth responses to monthly and seasonal climate variables but did not consider the potential role of extreme climatic events occurring at shorter time steps of days to weeks. Extreme weather events such as snow and ice storms (Lemieux and Filion 2004), thaw-freeze cycles (Auclair et al. 1996), extreme droughts (Breshears et al. 2005), and wind storms (Schlyter et al. 2006), affect forest productivity

and can lead to tree mortality. Furthermore, the incidence of extreme weather events have increased over the 20th century and are expected to increase further under climate change in the 21st century (IPCC 2007). Thus, examining the role of severe climatic events can improve the accuracy of climatically-sensitive forest simulation models.

Overall, the growth-climate relationships identified in this dissertation represent initial steps towards the fuller development and parameterization of climatically-sensitive growth and yield models for lodgepole pine which will help guide the sustainable management of lodgepole pine forest resources (Misson et al. 2004).

References

Auclair, A.N.D., Lill, J.T., and Revenga, C. 1996. The role of climate variability and global warming in the dieback of northern hardwoods. Water, Air and Soil Pollution, **91**: 163-186.

Barber, V. A., Juday, G.P., and Finney, B.P. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature, **405**: 668-73.

Bigler, C., and Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. Ecological Applications, **14**: 902-914.

Bouriaud, O., Breda, N., Dupouey, J.L., and Granier, A. 2005a. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. Canadian Journal of Forest Research, **35**: 2920-2933.

Bouriaud, O., Leban, J.-M., Bert, D., and Deleuze, C. 2005b. Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiology, **25**: 651-660.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences U.S.A., **102**: 15144-15148.

Brooker, R.W. 2006. Plant-plant interactions and environmental change. New Phytologist, **171**: 271-284.

Carroll, A.L., Régnière, J., Logan, J.A., Taylor, S.W., Bentz, B., and Powell, J.A. 2006. Impacts of climate change on range expansion by the mountain pine beetle. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Mountain Pine Beetle Initiative Working Paper 2006-14.

D'Arrigo, R.D., Jacoby, G.C., and Free, R.M. 1992. Tree-ring width and maximum latewood density at the North American tree line: parameters of climatic change. Canadian Journal of Forest Research, **22**: 1290-1296.

Das, A.J., Battles, J.J., Stephenson, N.L., and van Mantgem, P.J. 2007. The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. Canadian Journal of Forest Research, **37**: 580-597.

Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., and Bergeron, Y. 2001. Future fire in Canada's boreal forests: paleoecology results and general circulation model – regional climate model simulations. Canadian Journal of Forest Research, **31**: 854-864.

Fonti, P., Cherubini, P., Rigling, A., Weber, P., and Biging, G. 2006. Tree rings show competition dynamics in abandoned *Castanea sativa* coppices after land-use changes. Journal of Vegetation Science, **17**: 103-112.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, UK.

Gagen, M., McCarroll, D., and Edouard, J.-L. 2006. Combining ring width, density and stable carbon isotope proxies to enhance the climate signal in tree-rings: an example from the southern French Alps. Climatic Change, **78**: 363-379.

Goldblum, D., and Rigg, L.S. 2005. Tree growth response to climate change at the deciduous-boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research, **35**: 2709-2718.

Gower, S.T., Isebrands, J.G., and Sheriff, D.W. 1995. Carbon allocation and accumulation in conifers. *In* Resource physiology of conifers. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 217-254.

Hanninen, H. 2006. Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. Tree Physiology, **26**: 889-898.

Hanninen, H., Beuker, E., Johnsen, O., Leinonen, I., Murray, M., Sheppard, L., and Skroppa, T. 2001. Impacts of climate change on cold hardiness of conifers. *In* Conifer Cold Hardiness. *Edited by* S. Colombo and F. Bigras. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 305-333.

Havranek, W.M., and Tranquillini, W. 1995. Physiological processes during winter dormancy and their ecological significance. *In* Ecophysiology of coniferous forests. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, CA. pp. 95-124.

Hogg, E.H., and Bernier, P.Y. 2005. Climate change impacts on drought-prone forests in western Canada. Forestry Chronicle, **81**: 675-682.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research, **35**: 610-622.

IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on

Climate Change. *Edited by* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. Cambridge University Press, Cambridge, UK.

Kagawa, A., Sugimoto, A., and Maximov, T.C. 2006. $^{13}CO_2$ pulse-labelling of photoassimilates reveals carbon allocation within and between tree rings. Plant, Cell and Environment, **29**: 1571-1584.

Kagawa, A., Sugimoto, A., Yamashita, K., and Abe, H. 2005. Temporal photosynthetic carbon isotope signatures revealed in a tree ring through $^{13}CO_2$ pulse-labelling. Plant, Cell and Environment, **28**: 906-915.

Kolb, P.F., and Robberecht, R. 1996. High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. Tree Physiology, **16**: 665-672.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, San Diego, CA.

Lacointe, A. 2000. Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. Annals of Forest Science, **57**: 521-533

Lemieux, C., and Filion, L. 2004. Tree-ring evidence for a combined influence of defoliators and extreme climatic events in the dynamics of a high-altitude balsam fir forest, Mount Megantic, southern Quebec. Canadian Journal of Forest Research, **34**: 1436-1443.

Loader, N.J., Robertson, I., and McCarroll, D. 2003. Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. Palaeogeography, Palaeoclimatology, Palaeoecology, **196**: 395-407.

Loehle, C. 2003. Competitive displacement of trees in response to environmental change or introduction of exotics. Environmental Management, **32:** 106-115.

Loehle, C., and LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling, **90**: 1-31.

Manion, P.D. 1991. Tree disease concepts, 2nd edition. Prentice-Hall, Upper Saddle River, NJ.

McCarroll, D., and Loader, N.J. 2004. Stable isotopes in tree rings. Quaternary Science Reviews, **23**: 771-801.

Misson, L., Rathgeber, C., and Guiot, J. 2004. Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model. Canadian Journal of Forest Research, **34**: 888-898.

Monserud, R.A., Huang, S., Yang, Y. 2006. Predicting lodgepole pine site index from climatic parameters in Alberta. Forestry Chronicle **82**: 562-571.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. Government of Alberta, Pub. No. T/852.

Ogle, K., Whitman, T.G., and Cobb, N.S. 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. Ecology, **81**: 3237-3243.

Ogren, E. 2001. Effects of climatic warming on cold hardiness of some northern woody plants assessed from simulation experiments. Physiologia Plantarum, **112**: 71-77.

Ogren, E., Nilsson, T., and Sundblad, L.-G. 1997. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. Plant, Cell and Environment, **20**: 247-253.

Pedersen, B.S. 1998. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology, **79**: 79-93.

Pinto, P.E., Gegout, J-C., Herve, J.-C., and Dhote, J.-F. 2007. Changes in environmental controls on the growth of *Abies alba* Mill. in the Vosges Mountains, north-eastern France, during the 20th century. Global Ecology and Biogeography, **16**: 472-484.

Schlyter, P., Stjernquist, I., Barring, L., Jonsson, A.M., and Nilsson, C. 2006. Assessments of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. Climate Research, **31**: 75-84.

Skomarkova, M.V., Vaganov, E.A., Mund, M., Knohl, A., Linke, P., Boerner, A., Schulze, E.-D. 2006. Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. Trees, **20**: 571-586.

Sparks, J.P., and Black, R.A. 2000. Winter hydraulic conductivity and xylem cavitation in coniferous trees from upper and lower treeline. Arctic, Antarctic, and Alpine Research, **32**: 397-403.

Spittlehouse, D.L. 2005. Integrating climate change adaptation into forest management. Forestry Chronicle, **81**: 691-695.

Suarez, M.L., Ghermandi, L., and Kitzberger, T. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. Journal of Ecology, **92**: 954-966.

Volney, W.J.A., and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. Agriculture, Ecosystems and Environment, **82**: 283-294.

Wang, G.G., Chhin, S., and Bauerle, W.L. 2006. The effect of natural atmospheric CO_2 fertilization suggested by open-grown white spruce in a dry environment. Global Change Biology, **12**: 601-610.

Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., and Aitken, S.N. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology, **12**: 2404-2416.

Watson, E., and Luckman, B.H. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. Canadian Journal of Forest Research, **32**: 1858-1874.

Zweifel, R., Zimmermann, L., Zeugin, F., and Newbery, D.M. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. Journal of Experimental Botany, **57**: 1445-1459.

Appendix I: Validation statistics of regression models (developed in Chapter III: Tables 3-3, 3-4, and 3-5) relating basal area growth index with climatic variables across elevational regions (ERs) and diameter classes (DCs) and for all 65 sites combined.

ERs/	Mean temperature			Precipitation			Climate moisture index		
DCs	RMSE	SSE	PRESS	RMSE	SSE	PRESS	RMSE	SSE	PRESS
HL									
S	0.0936	0.674	0.731	0.0869	0.566	0.648	0.0854	0.547	0.629
M	0.0921	0.653	0.712	0.0871	0.569	0.652	0.0845	0.536	0.615
L	0.1005	0.778	0.845	0.0882	0.584	0.675	0.0848	0.540	0.630
T	0.0834	0.535	0.579	0.0805	0.486	0.565	0.0781	0.457	0.537
All	0.0868	0.581	0.631	0.0795	0.474	0.548	0.0769	0.444	0.516
FH									
S	0.0658	0.330	0.367	0.0723	0.402	0.430	0.0707	0.385	0.413
M	0.0608	0.281	0.314	0.0636	0.312	0.336	0.0619	0.295	0.319
L	0.0590	0.265	0.295	0.0605	0.282	0.305	0.0590	0.268	0.291
T	0.0550	0.230	0.257	0.0570	0.250	0.270	0.0545	0.228	0.247
All	0.0568	0.246	0.274	0.0602	0.279	0.301	0.0583	0.262	0.283
CH									
S	0.1693	2.179	2.449	0.1782	2.445	2.661	0.1725	2.261	2.494
M	0.1042	0.825	0.920	0.1113	0.954	1.040	0.1064	0.861	0.953
L	0.1473	1.650	1.807	0.1511	1.759	1.916	0.1451	1.599	1.746
T	0.1220	1.132	1.247	0.1312	1.326	1.449	0.1225	1.140	1.258
All	0.1210	1.112	1.232	0.1296	1.293	1.409	0.1224	1.138	1.248
RM									
S	0.0847	0.545	0.606	0.0833	0.534	0.575	0.0835	0.536	0.578
M	0.0738	0.414	0.457	0.0810	0.506	0.541	0.0794	0.485	0.518
L	0.0738	0.413	0.449	0.0755	0.439	0.465	0.0753	0.436	0.462
T	0.0691	0.363	0.392	0.0685	0.362	0.384	0.0690	0.367	0.388
All	0.0680	0.352	0.384	0.0699	0.376	0.400	0.0695	0.372	0.395
All									
S	0.0596	0.274	0.298	0.0647	0.322	0.344	0.0634	0.310	0.332
M	0.0569	0.249	0.271	0.0608	0.284	0.303	0.0593	0.271	0.290
L	0.0550	0.233	0.253	0.0594	0.271	0.289	0.0576	0.256	0.274
T	0.0504	0.196	0.212	0.0549	0.232	0.248	0.0532	0.218	0.233
All	0.0536	0.221	0.240	0.0582	0.261	0.278	0.0566	0.247	0.264

Note: ER abbreviations: HL, Boreal Highlands; FH, Foothills; CH, Cypress Hills; RM, Rocky Mountains; ALL, all ERs combined. DC abbreviations: S, small; M, medium; Large, large; T, top; ALL, all DC combined. Other abbreviations: RMSE, root mean squared error; SSE, error sum of squares; PRESS, prediction sum of squares.

Appendix II: Validation statistics of regression models (developed in Chapter IV: Figs. 4-3 and 4-4) relating growth variables (GV) at different positions and portions of the stem with climate variables across elevational regions (ERs) and diameter classes (DCs) and for all 65 sites combined.

	Mean temperature			Climate moisture index		
ER/GV	RMSE	SSE	PRESS	RMSE	SSE	PRESS
HL						
BH_{BAI}	0.0749	0.269	0.307	0.0699	0.230	0.269
AB_{VI}	0.0634	0.193	0.223	0.0547	0.141	0.170
US_{VI}	0.0565	0.150	0.174	0.0623	0.187	0.215
BH_{RI}	0.0800	0.301	0.361	0.0678	0.216	0.252
FH						
BH_{BAI}	0.0656	0.206	0.236	0.0655	0.206	0.234
AB_{VI}	0.0527	0.131	0.152	0.0603	0.175	0.200
US_{VI}	0.0529	0.135	0.150	0.0588	0.166	0.184
BH_{RI}	0.0448	0.096	0.110	0.0526	0.133	0.147
CH						
BH_{BAI}	0.1375	0.888	1.020	0.1398	0.919	1.058
AB_{VI}	0.1263	0.750	0.872	0.1304	0.799	0.938
US_{VI}	0.1393	0.931	1.070	0.1454	1.035	1.129
BH_{RI}	0.0960	0.442	0.502	0.1005	0.495	0.536
RM						
BH_{BAI}	0.0694	0.226	0.265	0.0724	0.252	0.283
AB_{VI}	0.0602	0.167	0.201	0.0671	0.216	0.240
US_{VI}	0.0727	0.248	0.288	0.0781	0.299	0.320
BH_{RI}	0.0501	0.118	0.136	0.0560	0.150	0.171
ALL						
BH_{BAI}	0.0593	0.169	0.193	0.0622	0.186	0.207
AB_{VI}	0.0499	0.117	0.137	0.0565	0.153	0.171
US_{VI}	0.0494	0.115	0.134	0.0562	0.152	0.170
BH_{RI}	0.0395	0.073	0.084	0.0496	0.118	0.130

Note: See Table 4-1 for abbreviations of elevational regions and Fig. 4-2 for growth variables. Other abbreviations: RMSE, root mean squared error; SSE, error sum of squares; PRESS, prediction sum of squares.

Appendix III: Intercorrelations between mean monthly temperature variables for all 65 sites combined (cf. Table 3-1).

	apr (t-1)	may (t-1)	jun (t-1)	jul (t-1)	aug (t-1)	sep (t-1)	oct (t-1)	nov (t-1)	dec (t-1)	jan (t)	feb (t)	mar (t)	apr (t)	may (t)	jun (t)	jul (t)	aug (t)	sep (t)	oct (t)
apr (t-1)	1.00																		
may (t-1)	**0.28**	1.00																	
jun (t-1)	0.04	0.06	1.00																
jul (t-1)	-0.01	0.01	0.08	1.00															
aug (t-1)	0.04	0.14	0.02	0.06	1.00														
sep (t-1)	-0.06	0.06	-0.07	0.07	-0.02	1.00													
oct (t-1)	0.10	0.08	0.16	0.01	-0.06	0.12	1.00												
nov (t-1)	0.13	0.14	-0.10	-0.11	0.06	0.15	0.04	1.00											
dec (t-1)	0.07	0.02	-0.15	0.05	-0.14	**0.27**	0.07	**0.25**	1.00										
jan (t)	0.16	-0.12	0.10	0.19	-0.06	-0.02	-0.04	-0.11	**0.27**	1.00									
feb (t)	0.20	-0.08	-0.13	-0.09	**0.25**	0.08	-0.03	0.11	0.05	0.20	1.00								
mar (t)	0.22	0.16	0.09	0.02	0.07	-0.12	0.03	0.03	0.07	**0.29**	0.03	1.00							
apr (t)	-0.07	-0.02	0.18	0.08	-0.01	0.10	-0.13	-0.03	-0.04	**0.23**	0.14	**0.28**	1.00						
may (t)	-0.08	-0.08	0.04	0.02	-0.11	0.00	-0.16	0.03	0.01	0.22	-0.17	**0.27**	**0.28**	1.00					
jun (t)	0.18	0.16	-0.03	-0.04	0.07	0.08	-0.05	0.06	0.20	0.10	-0.05	0.04	0.04	0.06	1.00				
jul (t)	-0.03	-0.19	0.08	0.06	-0.19	0.08	0.08	0.02	**0.23**	0.15	-0.16	-0.06	-0.01	-0.01	0.09	1.00			
aug (t)	-0.01	-0.02	0.11	0.12	-0.20	0.04	-0.04	-0.02	-0.02	0.20	0.01	0.09	0.04	0.12	0.03	0.10	1.00		
sep (t)	0.05	-0.05	-0.03	-0.08	-0.16	0.10	0.17	0.13	0.18	-0.09	-0.11	-0.04	-0.05	0.06	-0.07	0.07	-0.01	1.00	
oct (t)	0.10	0.02	-0.04	0.07	**-0.23**	0.00	0.16	0.10	**0.32**	0.16	-0.02	0.06	0.11	0.07	0.16	0.04	-0.03	0.13	1.00

Note: Correlation analysis conducted over the period of 1924-2003 and spanned two growing seasons from April of the prior year (t-1) to October of the current year (t). Correlation coefficients in bold are statistically significant at $p < 0.05$.

Appendix IV: Intercorrelations between total monthly precipitation variables for all 65 sites combined (cf. Table 3-1).

	apr (t-1)	may (t-1)	jun (t-1)	jul (t-1)	aug (t-1)	sep (t-1)	oct (t-1)	nov (t-1)	dec (t-1)	jan (t)	feb (t)	mar (t)	apr (t)	may (t)	jun (t)	jul (t)	aug (t)	sep (t)	oct (t)
apr (t-1)	1.00																		
may (t-1)	-0.07	1.00																	
jun (t-1)	-0.19	0.00	1.00																
jul (t-1)	0.08	0.21	0.02	1.00															
aug (t-1)	-0.13	0.14	0.02	0.02	1.00														
sep (t-1)	-0.13	0.15	0.01	-0.10	0.06	1.00													
oct (t-1)	0.06	-0.05	-0.14	-0.16	-0.15	-0.02	1.00												
nov (t-1)	0.16	0.13	-0.13	0.06	0.01	0.06	0.20	1.00											
dec (t-1)	-0.13	0.00	-0.12	-0.20	-0.07	-0.10	0.19	0.09	1.00										
jan (t)	0.10	-0.10	0.16	0.18	-0.12	**-0.23**	-0.06	0.01	0.04	1.00									
feb (t)	0.12	-0.09	0.01	-0.08	0.07	-0.05	-0.02	0.12	0.00	0.07	1.00								
mar (t)	0.17	0.02	-0.12	0.17	-0.13	-0.15	0.03	-0.02	-0.21	**0.30**	0.01	1.00							
apr (t)	0.02	-0.01	0.14	-0.10	0.06	0.10	-0.03	-0.02	-0.19	0.03	**0.28**	0.10	1.00						
may (t)	-0.03	0.08	0.14	-0.04	**0.28**	-0.02	-0.17	0.12	-0.12	-0.02	-0.10	-0.05	-0.08	1.00					
jun (t)	-0.16	0.04	0.02	0.18	-0.20	0.01	-0.05	-0.05	0.03	0.04	-0.16	0.09	-0.18	0.00	1.00				
jul (t)	**-0.25**	0.21	0.13	0.19	0.20	0.27	-0.05	-0.12	-0.01	0.00	-0.01	-0.09	0.02	0.22	0.03	1.00			
aug (t)	-0.04	-0.02	0.06	0.17	-0.03	-0.01	-0.12	0.01	0.10	0.12	0.10	-0.06	-0.16	0.14	0.04	0.04	1.00		
sep (t)	0.05	-0.13	-0.11	-0.20	-0.10	0.20	0.06	-0.10	-0.01	-0.05	-0.07	-0.09	-0.15	0.15	0.03	-0.09	0.06	1.00	
oct (t)	0.01	-0.08	-0.04	-0.18	0.00	-0.04	0.06	0.14	0.05	0.06	0.13	-0.15	0.08	-0.05	-0.13	-0.17	-0.18	-0.05	1.00

Note: Correlation analysis conducted over the period of 1924-2003 and spanned two growing seasons from April of the prior year (t-1) to October of the current year (t). Correlation coefficients in bold are statistically significant at $p < 0.05$.

Appendix V: Intercorrelations between monthly climate moisture index variables for all 65 sites combined (cf. Table 3-1).

	apr (t-1)	may (t-1)	jun (t-1)	jul (t-1)	aug (t-1)	sep (t-1)	oct (t-1)	nov (t-1)	dec (t-1)	jan (t)	feb (t)	mar (t)	apr (t)	may (t)	jun (t)	jul (t)	aug (t)	sep (t)	oct (t)
apr (t-1)	1.00																		
may (t-1)	0.04	1.00																	
jun (t-1)	-0.16	-0.06	1.00																
jul (t-1)	0.09	0.19	0.07	1.00															
aug (t-1)	-0.10	0.13	0.05	0.10	1.00														
sep (t-1)	-0.11	0.13	0.02	-0.08	0.03	1.00													
oct (t-1)	0.10	-0.04	-0.09	-0.17	-0.13	0.00	1.00												
nov (t-1)	0.15	0.11	-0.16	0.04	0.00	0.06	0.13	1.00											
dec (t-1)	-0.06	-0.02	-0.12	-0.16	-0.07	-0.03	0.16	0.06	1.00										
jan (t)	0.11	-0.18	0.12	0.21	-0.13	-0.15	-0.08	0.02	0.05	1.00									
feb (t)	0.15	-0.07	0.01	-0.11	0.12	0.02	-0.04	0.11	0.02	0.07	1.00								
mar (t)	0.19	0.09	-0.06	0.13	-0.17	-0.18	0.03	-0.05	-0.18	**0.31**	0.05	1.00							
apr (t)	-0.03	0.02	0.18	-0.03	0.05	0.11	-0.06	-0.01	-0.19	0.11	**0.32**	0.16	1.00						
may (t)	-0.04	0.07	0.10	0.00	0.21	-0.04	-0.21	0.17	-0.17	0.05	-0.08	0.00	0.05	1.00					
jun (t)	-0.11	0.21	0.07	0.19	-0.12	-0.01	-0.07	0.03	0.05	0.06	-0.15	0.06	-0.16	-0.07	1.00				
jul (t)	**-0.23**	0.15	0.16	**0.24**	0.18	0.20	-0.05	-0.11	0.01	0.02	-0.01	-0.09	0.05	0.19	0.07	1.00			
aug (t)	-0.01	-0.02	0.00	0.19	-0.03	0.02	-0.13	0.02	0.12	0.11	0.05	-0.02	-0.12	0.13	0.06	0.12	1.00		
sep (t)	0.08	-0.14	-0.05	-0.19	-0.14	0.14	0.09	-0.08	-0.01	0.00	-0.08	-0.11	-0.12	0.13	0.03	-0.08	0.03	1.00	
oct (t)	0.10	-0.07	-0.05	-0.11	-0.09	-0.04	0.10	0.19	0.14	0.06	0.07	-0.14	0.10	-0.04	-0.08	-0.17	-0.14	-0.02	1.00

Note: Correlation analysis conducted over the period of 1924-2003 and spanned two growing seasons from April of the prior year (t-1) to October of the current year (t). Correlation coefficients in bold are statistically significant at $p < 0.05$.